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Contribution to the taxonomy, bionomics and distribution of the Palaearctic *Celonites cyprius*-group (Hymenoptera, Vespidae, Masarinae) with the description of two new species from the North Caucasus and East Anatolia

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Abstract

Celonites ivanovi **sp. nov.** is described as a new species from Dagestan where it has been recorded from dry habitats in a small area on the northern side of the Greater Caucasus. *Celonites cagrii* **sp. nov.** is described from Erzurum Province in east Turkey. As in other members of the *C. cyprius*-group, the females of both species were observed to visit flowers of *Heliotropium* (Boraginaceae). A morphological examination including the male genitalia of all species of the *C. cyprius*-group revealed that *C. ivanovi* **sp. nov.** and *C. cagrii* **sp. nov.** share the apomorphic characters of this group and are closely related to *Celonites osseus* Morawitz, 1888. Mean genetic distance between *C. ivanovi* **sp. nov.** and *C. cagrii* **sp. nov.** based on COI-5 sequences is 7.40%. The geographical distribution of all members of the *C. cyprius*-group is summarized and an illustrated key is provided for the identification of males and females of the species. A lectotype is designated for *C. osseus*.

Keywords

Boraginaceae, distribution, flower visiting behaviour, *Heliotropium*, key to species, male genitalia, Palaearctic region, taxonomy, trophic relationships

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Introduction

The pollen wasp genus *Celonites* Latreille, 1802 forms a well defined monophylum (Carpenter 1993; Krenn et al. 2002) whose members share a number of distinctive characters such as the wide horizontal lamellae on the propodeum, the acute sides of the metasoma and the ability to roll up (Richards 1962; Gess and Gess 2010). The biogeographical distribution of *Celonites* is disjunct with 21 species occurring in the semi-arid to arid areas in the southwest of the Afrotropical region (Gess and Gess 2010) and approximately 42 species in the Palaearctic and adjacent dry areas in the north of the Afrotropical and Oriental region (according to the list of Carpenter 2001, combined with newly described or synonymized species by Gusenleitner 2002, 2007, 2012, 2018; Mauss 2013; Mauss et al. 2016; Mauss and Prosi 2018). Among the Palaearctic taxa of *Celonites* the subgenus *Eucelonites* Richards, 1962 is characterised by a small laterally directed process of the axilla which lies on the tegula or even fits into a slight emargination of the tegula opposite to the projection (Richards 1962). This unique apomorphy defines *Eucelonites* as a monophyletic group (Carpenter 2001; note that the nominate subgenus is evidently paraphyletic). Up till now 26 species and nine additional subspecies were assigned to this monophylum indicating high diversity. However, many of these taxa were described from small type series often containing only one sex and the last summarizing key provided by Richards (1962) left out several rarely collected species from the Middle East and Central Asia. Therefore, the identity and status of some described *Eucelonites* taxa is still uncertain and species identification can be difficult. Within *Eucelonites*, *Celonites cyprius* Saussure, 1854 and its closer relatives form a distinct group which is characterized by male genitalia with distally tapering more or less spatula-like harpides, the medial and lateral margin of which are partly raised ventrally in addition (Figs 12, 13). We suggest naming this group the *Celonites cyprius*-group.

The purpose of the present paper is to describe two new species of *Celonites* belonging to the *C. cyprius*-group from the Republic of Dagestan, Russia, and Erzurum Province in East Anatolia, Turkey, as well as to summarize taxonomic and chorological data on the related taxa and to provide a key for their identification.

Materials and methods

Field investigations of the hitherto unknown *Celonites ivanovi* sp. nov. were made by A. Fateryga on 23 June 2018 in the vicinity of Maydanskoye in the Untsukulskiy district of the Republic of Dagestan, Russia [locality 1: 42°37'36"N, 46°56'48"E], where 3 females were observed and 2 females were collected, and on 11 June 2019, 15 and 16 June 2021 at a second site in the vicinity of Maydanskoye, 3 km to the southeast of the first locality [locality 2: 42°36'07"N, 46°58'13"E], where numerous females and males were observed and 17 females and 10 males were collected. Wasp activity and

flower visiting behaviour were observed with the naked eye for approximately one hour in the morning of 11 June 2019 and documented with a Canon PowerShot SX160 IS camera. The pictures were compared to single frames of video sequences of *C. cyprius* and *C. rugiceps* Bischoff, 1928 visiting *Heliotropium* flowers in Rhodes (taken with a Canon EOS 80D, 50 frames per second, scale up to 1:1, Mauss et al. in prep.). Flower preferences of the wasps were studied by counting the number of sightings (= first observations) of flower visiting individuals while walking randomly across the locality. A single female was recorded on 22 June 2021 in the vicinity of Turtsi in the Lakskiy district [locality 3: 42°11'34"N, 47°09'33"E]. Field observations of *Celonites cagrii* sp. nov. were made by E. Yildirim at Şenkaya-Akşar in the Erzurum province of Turkey on 12 July, 14 July and 1 August 2020. For identification of the collected *Heliotropium* plants the keys provided by Grossheim (1967) and Dönmez (2008) were used.

For the morphological and chorological investigations in total 479 dry specimens of the *Celonites cyprius*-group were examined from the following collections: Museum of Zoology Lausanne, Switzerland (**MCZL**), Museum of Natural History Mainz, Germany (**NHM**), Natural History Museum of Venice, Italy (**MSNVE**), Upper Austrian State Museum – Biology Centre, Linz, Austria (**OLML**), State Museum of Natural History Karlsruhe, Germany (**SMNK**), Stuttgart State Museum of Natural History, Germany (**SMNS**), Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia (**ZISP**), Zoological Museum of the M.V. Lomonosov Moscow State University, Russia (**ZMMU**), as well as the private collections of A.V. Fateryga stored in the T.I. Vyazemsky Karadag Scientific Station – Nature Reserve of RAS – Branch of A.O. Kovalevsky Institute of Biology of the Southern Seas of RAS, Feodosia, Russia (**AF**), J. Gusenleitner, Linz, Austria (**JG**), V. Mauss, Michelfeld, Germany (**VM**), M. Schindler, Bonn, Germany (**MS**), C. Schmid-Egger, Berlin, Germany (**CSE**) and E. Yildirim, Erzurum, Turkey (**EY**) (Suppl. material 1: Table S1). Every specimen examined by V. Mauss was labelled with an individual, serial database number (**dbM** = database Mauss) printed on the determination label. The holotypes were deposited in OLML, paratypes in American Museum of Natural History (**AMNH**), OLML, ZISP, AF, VM and EY.

Specimens were investigated under a WILD M3 stereo microscope (maximum magnification 80 times). Numbers of terga and sterna apply to metasomal segments. Antennal articles are termed A1–A12 counted from the proximal to the distal end. Nomenclature of male genitalia follows that of Birket-Smith (1981). Measurements of the exoskeleton were made using an ocular micrometer (highest resolution 0.011 mm; microscope in monaxial position). Distances between the ocelli, the compound eyes and the mesonotum width were measured according to Eck (1978). Proportion of head width to head length in the key was calculated from measurements of the maximum distance between the lateral margins of the compound eyes and the distance in the median axis between the bottom of the ventral emargination of the clypeus and the dorsal end of the median ocellus, while the head was aligned with dorsal and median part of ventral margin of the clypeus in focus plane and the lateral margins of

the compound eyes in symmetrical distance to the median axis. Drawings were made with a drawing tube (WILD Type 308700) in monaxial position. For drawings of the postero-lateral part of the propodeum the metasoma was removed from the specimens. The postero-lateral part of the propodeum was viewed from dorso-posterior with the dorso-anterior border of the pronotum becoming just visible anteriorly, so that the dorsal area of the pronotum was visible at a flat angle, while the apical ends of the postero-lateral processes were orientated exactly transversal. Male genitalia were removed after resoftening of the specimens and studied in 80% ethanol or glycerine. Macrophotos of whole specimens were taken with a Canon EOS 80D camera with a 100 mm macro-lens and extension tube (scale more than 1:1, resolution 24 mega pixel) and macro flash-lights. Microphotos were taken with a Keyence VHX-5000 Digital Microscope (combined stacking and stitching). Photographs of the lectotype of *C. osseus* Morawitz, 1888 were taken in ZISP with a Canon EOS 70D camera mounted on an Olympus SZX10 stereomicroscope. Multifocus-pictures were generated with Helicon Focus 6 Pro software. Final illustrations were post-processed for sharpness, contrast, and brightness using Adobe Photoshop CS2 software.

DNA barcoding was accomplished by AIM Advanced Identification Methods GmbH Leipzig following standard methods of DNA extraction from a single leg of dry specimens or specimens collected and stored in 96% pure ethanol, PCR for Cytochrome Oxidase subunit 1 (COI-5P), cycle sequencing of forward and reverse strand and sequence editing. Nucleotide sequences of ten individuals from four taxa of the *C. cyprius*-group were obtained uploaded and compared to the BOLD database (www.BOLDsystem.org). Another eight COI-5P sequences of three taxa of the *C. cyprius*-group were obtained from the BCHYM- and GBACU-project by courtesy of Christian Schmid-Egger and Stefan Schmidt and added to the data set. Finally genetic distances (Kimura 2 Parameter) and a neighbour joining BOLD TaxonID Tree were computed including 18 COI-5P sequences of morphologically identified specimens of *C. cagrii* sp. nov., *C. cyprius*, *C. ivanovi* sp. nov., *C. rugiceps* and *C. yemenensis* Giordani Soika, 1957 using the following parameters: distance model Kimura 2 Parameter; pairwise deletion of positions containing gaps and missing data; minimum complete overlap 100 bp; alignment with BOLD Aligner (Amino Acid based HMM); individual nucleotide sequence length 557–699 bp.

For the investigation of the geographic distribution label information of 479 specimens of the *C. cyprius*-group coming from 114 localities was entered into the database Mauss (Suppl. material 1: Table S1). Additionally, 55 published records were taken from Bischoff (1928), Blüthgen (1952), Bytinsky-Salz and Gusenleitner (1971), Carpenter (2001), Ebrahimi and Carpenter (2008), Giordani Soika (1957), Gusenleitner (1966, 1973, 1997, 2005, 2010), Richards (1962, 1984) and Schmid-Egger (2017) (Suppl. material 1: Table S1). If not given on the label or in the publication, WGS 84 coordinates were reconstructed mainly with the aid of Google Maps (www.google.de/maps). The distribution map was created with Natural Earth (www.naturalearthdata.com) using the open-source geographic information system QGIS, version 3.4 (www.qgis.org).

Systematics

Celonites osseus Morawitz, 1888

Celonites osseus Morawitz, 1888: 268–269, ♀, type locality: "territorio transcaspico (Tschikischljar) [Turkmenistan]", **lectotype (designated here):** ♀, <golden disc>, "Tschikischljar. Pom.[eranzev]", "*Celonites osseus* ♀. F. Moraw.", "к. Ф Моравица [coll. F Morawitz]", "Lectotypus ♀ *Celonites osseus* Morawitz des. Fateryga, 2018 <red label>" ZISP (Fig. 3a–c); Kostylev, 1935: 114, Turkestan, Transcaspian sands, Armenia; Richards, 1962: 216 (key), 226–227, Turkmenistan (Repetek), misidentification of *Celonites crenulatus* Morawitz, 1888 not *C. osseus*; Carpenter, 2001: 11, Armenia, Turkmenistan.

Additional material studied. Armenia: Zanga [currently Hrazdan] River, near Yerevan, 19.07.1935 1♀ (dbM 5855) leg. G. Kostylev ZMMU; Yerevan, Nork [=Nor Nork], 23.06.1930 1♀ leg. A. Shelkovnikov ZISP. **Turkmenistan, Balkan region:** Krasnovodsk [currently Türkmenbaşy], 13.06.1928 1♀ leg. V. Gussakovskij ZISP, 16.06.1928 1♂ leg. V. Gussakovskij ZISP; Jebel, 25 km NW Balkanabat, 22.05.1993 1♂ (dbM 5521) leg. M. Halada OLML. **Iran:** Elburz, 30 km S of Ab Ali, 09.07.1965 1♀ (dbM 5788) leg. Giordani Soika & Mavromoustakis MSNVE; Elburz, Vana 50 km N di Ab Ali, 12–13.07.1965 10♀♀ (dbM 5676, 5677, 5678, 5780, 5781, 5782, 5783, 5784, 5785, 5786) leg. Giordani Soika & Mavromoustakis MSNVE; Elburz (Mazandaran), Pulour [=Polour] 22 km N of Ab Ali, 13–14.07.1965 1♀ (dbM 5787) leg. Giordani Soika & Mavromoustakis MSNVE; Fars, Daria Namak, steppe presso lago salato 27 km E Shiraz, 07.07.1965 3♀♀ (dbM 5679, 5778, 5779) leg. Giordani Soika & Mavromoustakis MSNVE; Fars prov., 20 km E Kazarun, 29°33.034'N, 51°49.416'E, 1256 m, 14.06.2019 1♂ leg. V.M. Gnezdilov ZISP; Golestan prov., 70 km E Minudasht, 1050 m, 12.06.2010 1♀ (dbM 4617) leg. M. Halada OLML; Teheran, Steppa presso Chitgar, 18 km W di Teheran, 15.07.1965, 1♀ (dbM 5675) leg. Giordani Soika & Mavromoustakis MSNVE.

Taxonomic remarks. The identity of *C. osseus* was probably not clear to O.W. Richards, since in his key and in his description of the species he emphasizes that the dorsal area of the mesoscutum has smooth shining interstices at least as wide as the punctures, which is clearly inconsistent with the original description of Morawitz (1888: 269), and that the metasomal terga II–V are not at all crenulated (Richards 1962: 216, 227). Moreover, the measurements given by him for the length of body and fore-wing seem to be too large to represent *C. osseus*. His description was based on a single female from Repetek collected on 7 June 1937 by G. Kostylev placed in ZMMU and determined by Kostylev as *C. osseus* (Richards 1962: 227). However, this particular specimen is lacking in the ZMMU, but there is another female (dbM 5854) from Repetek collected on 9 June 1937 labelled by Kostylev as *C. osseus*, which is clearly misidentified and belongs to *Celonites crenulatus* Morawitz, 1888 or an undescribed taxon close to it. The description of *C. osseus* given by Richards (1962: 226–227) is

almost identical with the characters of this misidentified specimen. Moreover, there is a series of seven correctly identified males of *C. crenulatus* in the collection of the ZMMU collected on 1 and 9 June 1937 at Repetek by G. Kostylev, while genuine specimens of *C. osseus* are lacking from this locality. Obviously, Kostylev misinterpreted two females of his *C. crenulatus* series with weak crenulation on the metasomal terga as *C. osseus*. Almost certainly, Richards investigated one of these wrongly identified specimens (maybe it was given to him, because it was the only duplicate specimen identified as *C. osseus* in the collection of the ZMMU) and finally based his description on it. As a consequence, the key and the description provided by Richards (1962) cannot be used for the identification of *C. osseus*.

Distribution. Armenia, Turkmenistan, Iran (new record) (Fig. 17).

Bionomics. Unknown.

Figure 1. Imagines of the *C. cyprius*-group in lateral view, proboscis protruded (*C. rugiceps* female dbM 5447 male dbM 5450, *C. cyprius* female dbM 5428 male dbM 5434).

***Celonites cagrii* Mauss & Yildirim, sp. nov.**
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Holotype. ♀ (dbM 5610) "[Turkey] TR-Erzurum Şenkaya-Akşar [40.648262°N, 42.342351°E] 14.VII.2020-1275 m Leg. E. Yildirim [on *Heliotropium ellipticum* Ledeb.]" OLML, BOLD process ID CECYP006-20.

Paratypes. "[Turkey] TR-Erzurum Şenkaya-Akşar [40.648262°N, 42.342351°E] 20.VIII.2011-1275 m Leg. E. Yildirim" 1♀ (dbM 4574) EY; "[Turkey] TR-Erzurum Şenkaya-Akşar [40.648262°N, 42.342351°E] 12.VII.2020-1275 m Leg. E. Yildirim [on *Heliotropium ellipticum* Ledeb.]" 3♀ (dbM 5607, 5608 (BOLD process ID CECYP005-20), 5609) VM; "[Turkey] TR-Erzurum Şenkaya-Akşar [40.648262°N, 42.342351°E] 01.VIII.2020-1275 m Leg. E. Yildirim [on *Heliotropium ellipticum* Ledeb.]" 1♀ (dbM 5616) AMNH, 1♂ (dbM 5619) 3♀ (dbM 5611, 5612, 5615) VM, 4♀ (dbM 5613, 5614, 5617, 5618) EY; "ARMENIA Erevan Monti desertici Aighepat 40 Km. SE 23-VII-63 [leg. Giordani Soika]" 2♂♂ (dbM 5789, 5790) MSNVE.

Diagnosis. See key.

Description. Female. Colour (Figs 2, 4f): Black. The following are light yellowish-white: rectangular spot dorso-medial on clypeus; large spot on each ocular sinus dorso-medially extending over lateral part of frons; medium-sized spot on antero-dorsal angle of pronotum (humeral spot); broad stripe along dorso-medial (inner) margin of pronotum, anteriorly somewhat angularly enlarged with little median dent; small irregular postero-medial spot on mesoscutum; large spot on dorsal mesepisternum; laterally directed process of axilla; medium-sized narrow transversal spot postero-medial on scutellum; dorsal and ventral side of propodeal lamella; antero-lateral one-fifth and posterior two-fifth of tegula, interrupted by brownish translucent area on bulge; posterior band on tergum I occupying whole of sides but less than half of middle part, somewhat widened anteriorly in median axis, anteriorly with small brownish tinge towards adjacent black area; laterally and medially widened posterior bands on terga II–V, anteriorly with small brownish tinge towards adjacent black area, interrupted on each side of middle by blackish area; two weak minute little spots medial on tergum VI; outside of distal tips of fore-, mid- and hind-femora; outside of proximal third to half of fore-, mid- and hind-tibia and little marking on outside at distal end of mid-, and hind-tibia. Brown are: distal half of mandible; maxillary and labial palpi, protrudeable parts of proboscis; ventral margin of labrum; postero-lateral margin of scutellum; median third of metanotum; postero-lateral process of propodeum; humeral plate; posterior translucent margin of tergum VI; tarsi; sterna I–V, posterior margin of sterna II–V translucent. Antenna black except: yellowish white markings medial on A4–A7 and proximal part of A8; brown-suffused area ventral on A10–A11. Wings moderately infuscate, pterostigma blackish-brown, veins blackish-brown becoming somewhat lighter at base.

Variation (number of differing specimens in brackets): Light yellowish-white markings: spot on each ocular sinus dorso-medially separated from spot on lateral part of frons (1); frons with two isolated little (4) or medium-sized (2) spots above antennal sockets, or both spots above antennal sockets large and dorso-laterally fused with

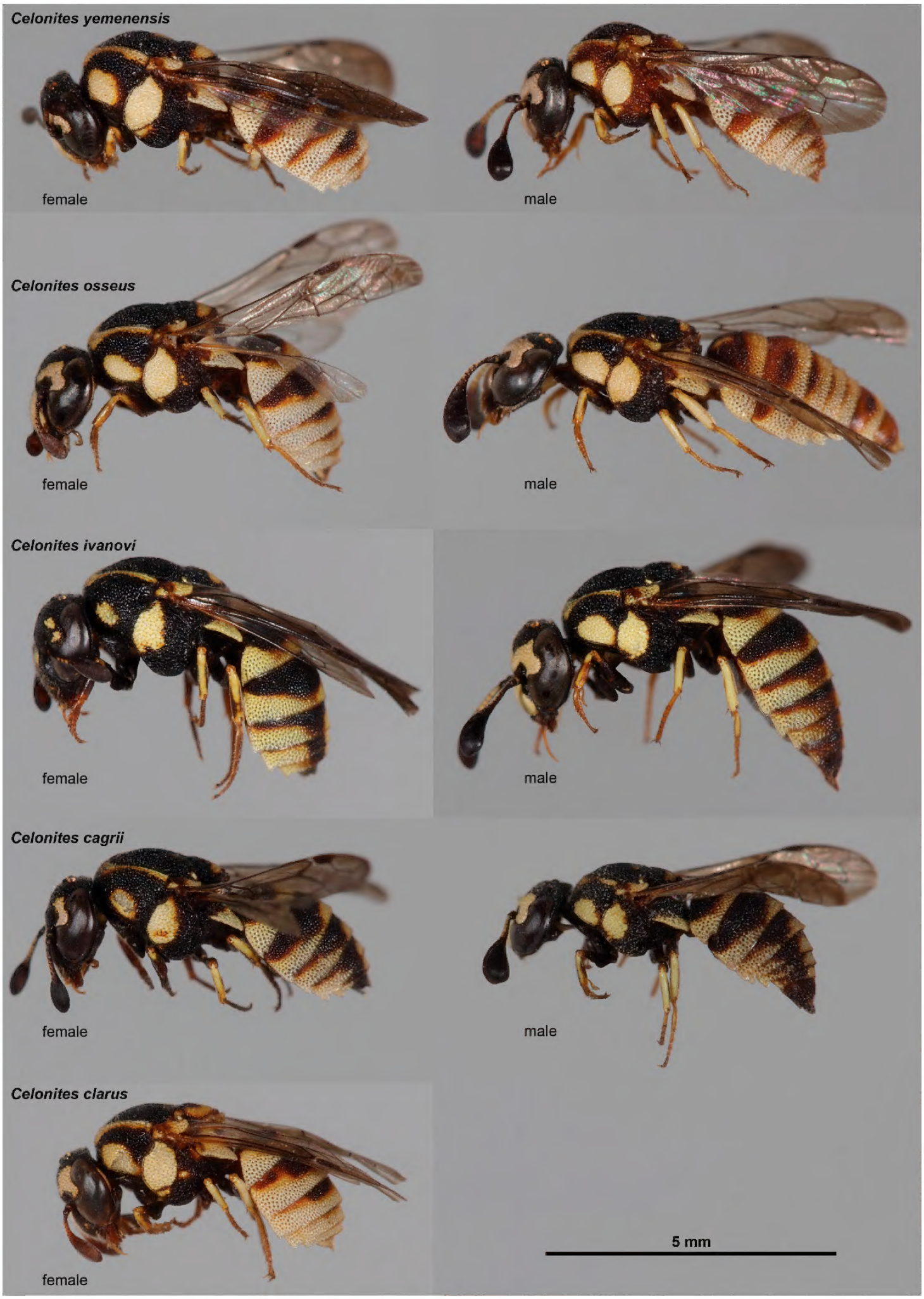

Figure 2. Imagines of the *C. cyprius*-group in lateral view, proboscis retracted (*C. yemenensis* female dbM 4944 male dbM 4945, *C. osseus* female dbM 4617 male dbM 5521, *C. ivanovi* sp. nov. female dbM 5493 male dbM 5498, *C. cagrii* sp. nov. female dbM 5607 male dbM 5619, *C. clarus* female dbM 5674).

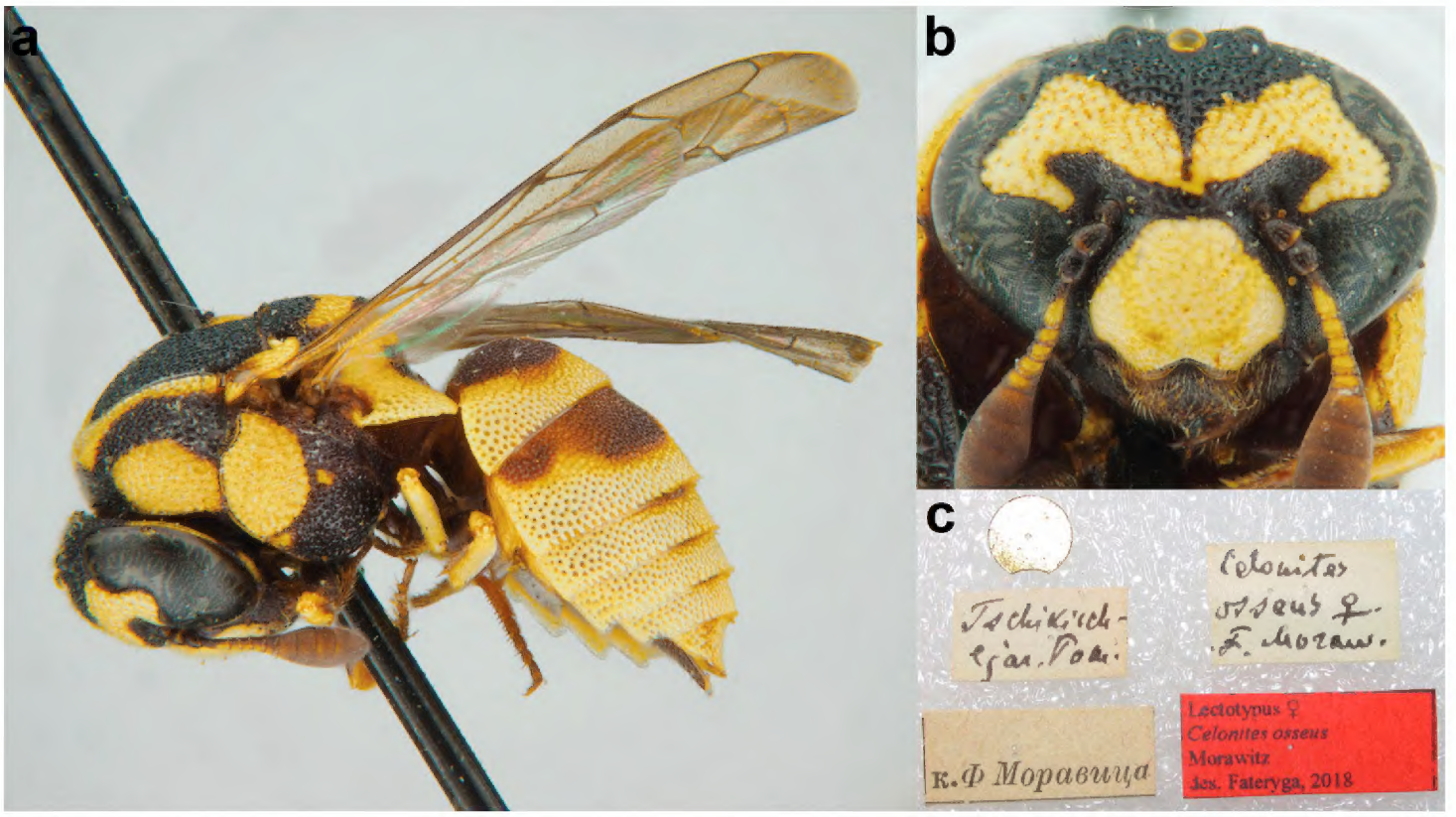

Figure 3. Lectotype of *Celonites osseus* **a** lateral view **b** head in frontal view **c** labels.

large marking extending from ocular sinus over lateral part of frons (1); continuous narrow stripe on gena and postgena along occipital carina from dorso-lateral corner of head to postero-ventral corner of compound eye (1), this stripe can be shortly interrupted (1) or reduced to short narrow spot on gena and postgena along occipital carina at dorso-lateral corner of head (3) and/or little spot on postgena adjacent to occipital carina level with postero-ventral corner of compound eye (7); minute spot on malar area above condylus (7); humeral spot small (2); little spot antero-dorsally on ventral mesepisternum (2); mesoscutum completely black (1) or with rectangular spot (2) or triangular spot with top directing posteriorly (1); transversal spot postero-medial on scutellum large (2); narrow transversal stripe on median third of metanotum (10); minute spot on pointed protuberance on posterior face of propodeum dorsally on each side of middle (1); tergum I with little (1) or medium sized (1) separated longitudinal antero-medial spot that can be posteriorly fused with posterior band in median axis in addition (1); posterior band on tergum II (4) or on terga II–III (2) not completely interrupted along posterior margin on each side of middle; tergum VI with large medial spot and little spot on each postero-lateral angle (2) or only with large (5) or small (2) medial spot that can be reduced to four weak minute little dots (1); continuous stripe on outside of mid-tibia only (1) or on outside of mid- and hind-tibia (7). Other markings: light yellowish-white marking on A7 darkened (1); medial on proximal part of A8 only light brownish suffused (3) or with same colour than distal part (1).

Structure: Head in frontal view 1.50 times as wide as long in median (min 1.45, max 1.54, n=5) (Fig. 4f). Mandible with two large blunt incisivi at distal end separated by acute-angled cleft and two smaller more acute subapical incisivi on antero-medial

Figure 4. Female head in frontal view **a** *C. yemenensis* (dbM 5528) **b** *C. clarus* (dbM 4616) **c** *C. cyprius* (dbM 5431) **d** *C. osseus* (dbM 5678) **e** *C. ivanovi* sp. nov. (dbM 5490) **f** *C. cagrii* sp. nov. (dbM 5609).

margin. External side of mandible distally bearing longitudinal rows of long stiff setae; at base without distinct transverse depression; basal area with shagreened cuticula moderately covered with pubescence of tiny thin setae (longer than in *C. cyprius*); anterior to condylar ridge cuticula of basal area extends further apically becoming distinctly striated in longitudinal direction; this area contrasts to smooth shiny but somewhat longitudinally striated cuticula on condylar ridge and postero-apically adjoining surface; condylar ridge distinct at basal two-third of mandible continuing in more gentle curve into apical side (strongest bend approximately after basal third of mandible). Labrum matt shining, finely shagreened and longitudinally wrinkled; densely covered with pale stiff setae directing obliquely downwards; setae as long as A7 maximum wide, with distal end curved ventro-medially, laterally at apex of labrum thicker with larger diameter at base. Clypeus 1.4 times wider than long; translucent ventro-medial margin becoming much narrower medially resulting in distinct median emargination; cuticula shiny, ventro-medially above emargination smooth with sparse micropunctation becoming moderately spaced dorsally and laterally on disc with larger irregular flat depressions and wrinkles in addition; dorso-lateral vertical parts of clypeus smooth with moderately spaced micropunctation partly striated at base; covered with pale thin stiff setae arising from micropunctures; setae on disc about as long as A4, vertically erected with distal ends strongly curved in ventro-medial direction, on sides shorter lying more flatly. Frons very coarsely punctured, interstices shining, raised to ±transversal little rounded ridges; protruding central part of supra-antennal area smooth, with moderately to sparsely spaced macropunctures and few micropunctures; semi-circular depression of antennal groove wrinkly shagreened; slight median depression dorsal to supra-antennal area, frontal line weak; sparsely covered with pale short setae arising from coarse punctures. Vertex with close macropunctation, becoming more closely reticulate behind ocelli with smaller punctures and interstices more strongly raised forming short sharp-edged ±transversal ridges; sparsely covered with pale short setae arising from punctures; cuticula of interstices shiny not shagreened (Fig. 5f). Median ocellus 1.2 times larger in diameter than lateral ocelli; median ocellus somewhat bilateral symmetric with anterior sector less strongly curved than posterior sector; lateral ocelli ±circular (in dorso-lateral view). Compound eyes sparsely covered with tiny setae. Preoccipital carina sharp; medially straight, nearly transversal; laterally behind dorso-lateral end of each compound eye curved downwards for short distance becoming obsolete posterior to dorsal end of postocular carina. Gena narrow, less than half as wide as basal width of A3. Postocular carina sharp; extends dorsad from posterior mandibular articulation along posterior margin of gena; ends level with dorsal end of compound eye anterior to preoccipital carina that runs parallel for short distance. Antennal articles A8–A12 forming ventrally flattened club about 2.0–2.2 times as long as broad (in dorsal view).

Pronotum with anterior margin raised to carina; anterior pronotal carina (*sensu* Carpenter 1988) in antero-ventral area of pronotum weak, forming anterior sharp edge along ventral half of crenate groove dorsally continuing into sharply bent but

Figure 5. a, b Female clypeus in frontal view **a** *C. cyprius* (dbM 5431) **b** *C. ivanovi* sp. nov. (dbM 5490) **c, d** female mandible outside **c** *C. cyprius* (dbM 5431) **d** *C. ivanovi* sp. nov. (dbM 5490) **e, f** female ocelli and vertex in dorsal view **e** *C. ivanovi* sp. nov. (dbM 5492) **f** *C. cagrii* sp. nov. (dbM 5609).

rounded anterior border of crenate groove; crenate groove straight small trough-like, with nearly vertical anterior and posterior wall running parallel, bottom with sulcature of transverse ribs; running at very acute angle along posterior margin of pronotum slightly diverging from the posterior margin dorsally; cuticula between posterior margin of crenate groove and posterior margin of pronotum at same level as surrounding surface, shiny, with some micropunctures; on lateral quarter distinct posterior pronotal carina sharply separating semicircular antero-ventral area from dorsal area of pronotum; antero-medial front behind head nearly vertical; slight depression along dorso-medial margin especially anteriorly; posterior margin raised to short translucent carina dorsally in front of upper half of tegula; cuticula of antero-ventral area shiny, shagreened, with few small shallow punctures; cuticula of dorso-lateral area shiny, with close coarsely reticulate macropunctation, smooth interstices raised to narrow edges postero-laterally forming lines; cuticula of pronotal lobe and dorsally continuing concavely curved depression in front of tegula smooth with a few distinct punctures but without reticulation, ventro-laterally more distinctly set off from adjacent parts of pronotum than dorsally. Mesoscutum with distinct median notal suture on anterior third; cuticula shiny, coarsely reticulate with close deep macropunctation and narrow, distinctly raised interstices. Mesoscutellum with distinct transverse sulcature of longitudinal cuticula-ribs separated by intercostal spaces along antero-medial margin; laterally with distinct smooth carina along posterior margin, carina medially increasingly reduced so that cuticula of medial lobe continues evenly into crenulate margin; cuticula more coarsely reticulate than on mesoscutum. Metanotum laterally with distinct sulcature of longitudinal cuticula-ribs separated by intercostal spaces; carina along posterior margin medially with small irregular indentations continuing in vertical median keel. Axilla produced into curved tapering projection which fits into slight emargination of tegula. Tegula shiny, closely covered by macropunctures except completely smooth central convex area. Antero-ventral parts of pronotum, ventral corner of dorsal mesepisternum and ventral mesepisternum form continuous antero-ventral cavity delimited from lateral parts of mesosoma by posterior pronotal carina, carina along ventral margin of dorsal mesepisternum and epicnemial carina. Dorsal mesepisternum separated from ventral mesepisternum by weak mesepisternal groove; with distinct carina along ventral margin, which is in one line with epicnemial carina though separated from it by little notch. Ventral mesepisternum with pronounced epicnemial carina, posteriorly deflexed backwards running medially in a curve to front of mid-coxa. Mesepimeron feebly separated by weak scrobal groove; postero-ventrally bearing mesopleural process of moderate size, distally rounded, its posterior side shagreened matt shiny without punctures. Cuticula laterally on mesopleurum and dorsal metapleurum shiny, with closely reticulate macropunctation; longitudinally striated by raised interstices in parts; ventral mesepisternum coarsely punctured with some interstices strongly raised to knife-like edges forming coarse rugose sculpture. Propodeum with horizontal propodeal triangles and dorso-lateral margins of posterior face of propodeum reduced to two pointed protuberances dorsally on each side of

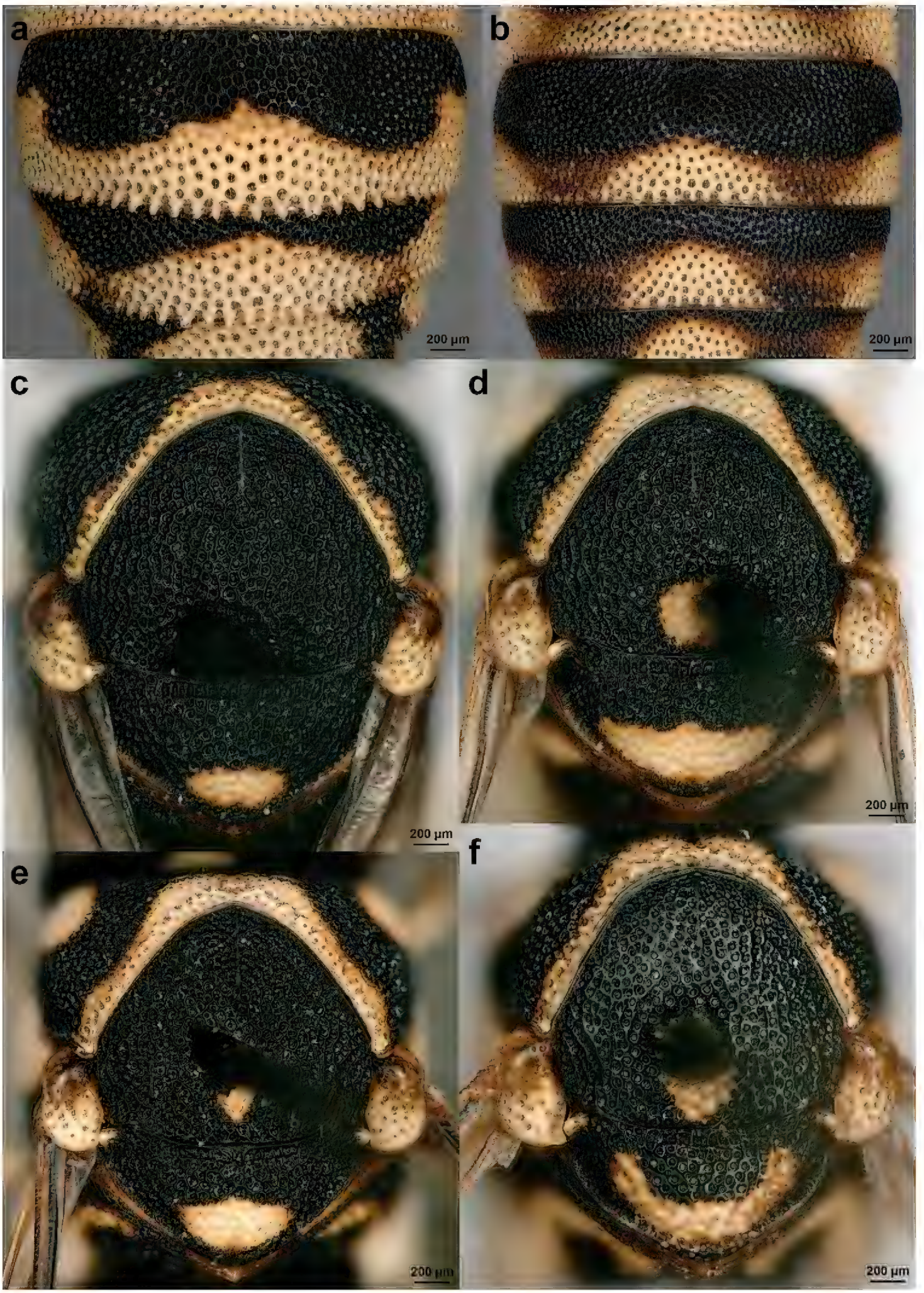

Figure 6. a, b Metasomal tergum II and III of female in dorsal view **a** *C. rugiceps* (dbM 5446) **b** *C. ivanovi* sp. nov. (dbM 5481) **c–f** mesonotum of female in dorsal view **c** *C. ivanovi* sp. nov. (dbM 5492) **d** *C. osseus* (dbM 4617) **e** *C. yemenensis* (dbM 5528) **f** *C. clarus* (dbM 4616).

middle, cuticula on protuberances rugose with interstices raised to knife-like edges; posteriorly with narrow medial cuticula-fold running from dorsal margin to postero-medial flange of propodeum; posterior surface ventrally striated by strong vertical cuticula-folds arising below anterior transversal carina of postero-medial flange of propodeum, with shallow macropunctures between folds, moderately covered with fine pale setae arising from macropunctures, laterally and dorsally continuing into coarsely reticulate macropunctation with shorter setae. Cuticula below lateral lamella shiny, on metepisternum densely horizontally wrinkled, on side of propodeum shagreened with moderately spaced small shallow punctures. Lateral lamella moderate, slightly curved laterally downwards, its outer margin gently curved, its apex truncate, outer and posterior margins somewhat crenate; inner margin of lateral lamella and lateral apex of postero-lateral process of postero-medial flange of propodeum separated by small gap; anterior margin of postero-lateral process straight transverse, while posterior margin converges in weak curve towards lateral apex; outline of emargination being broad at its base with short narrow neck between lateral apex of postero-lateral process and inner margin of lateral lamella and small oval-rounded apical part (Fig. 7c); dorsal cuticula of lateral lamella and adjacent dorso-lateral part of propodeum shiny, with reticulate macropunctation. On whole exoskeleton single thin seta arises from bottom of each macropuncture, seta short if not stated otherwise.

Fore-femur postero-ventrally produced in middle forming anteriorly curved lobe distally changing into tapering carina along ventral margin of femur; end of tibia when folded against femur coinciding with produced region; tarsomeres I–IV broad and flattened; underside of tibia and tarsomere I with strong obliquely distally directing setae forming stiff brush; underside of tarsomere I and II with comb-like row of particularly strong setae along distal margin. Claws ventrally with small tooth.

Metasomal terga with postero-lateral corners slightly produced; posterior margin of tergum I weakly crenulated, crenulation not produced into spines and not projecting over smooth translucent lower posterior margin of tergum; posterior margin of terga II–V weakly to moderately crenulated, crenulation in middle of terga II–IV produced into little slightly raised teeth projecting approximately to end of translucent lower posterior margin of terga; cuticula moderately shining, densely covered with reticulate macropunctation, punctures distinct, smaller and more regular than on mesoscutum; interstices finely shagreened. Tergum VI with lateral margins converging in weakly convex, nearly straight or slightly concave curve, at transition to posterior median lobe strongly bend inwards forming distinct postero-lateral angle on each side; posterior margin of posterior median lobe running in convex oval curve formed by distinct translucent lamella; posterior median lobe set off from more strongly sloping median area of tergum VI by well-definded concave curvature at its base; cuticula covered with fine pubescence of thin pale setae arising from micropunctures on interstices of reticulate macropunctation, slightly projecting beyond postero-median translucent lamella and lateral margins; on ventral side (viewed from ventral) posterior translucent lamella of median lobe continues on both sides into distinct carina running anteriorly

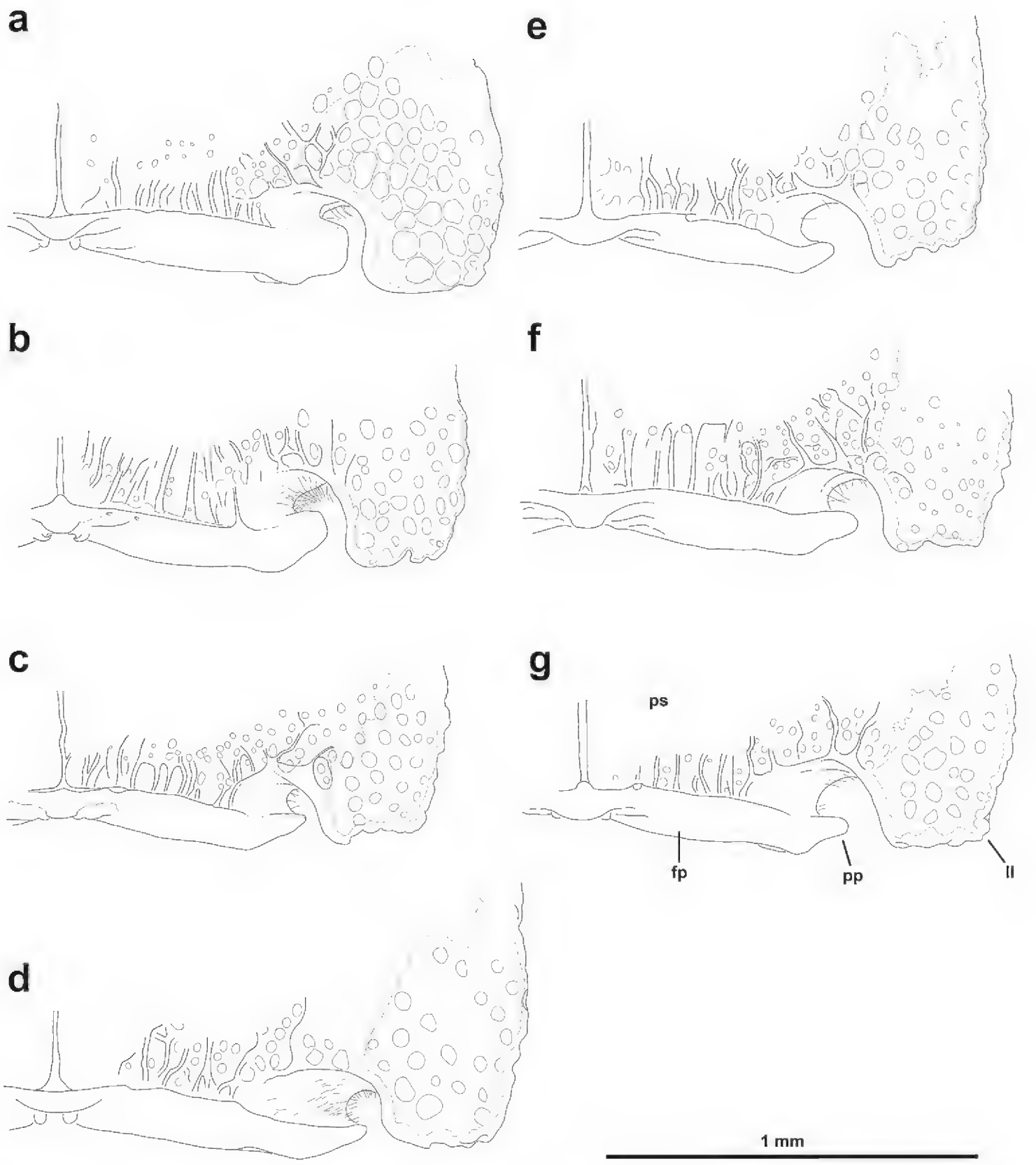

Figure 7. Right side of postero-lateral part of the propodeum of females in dorso-posterior view **a** *C. yemenensis* (dbM 4759) **b** *C. clarus* (dbM 4616) **c** *C. cagrii* sp. nov. (dbM 5611) **d** *C. rugiceps* (dbM 5446) **e** *C. cyprius* (dbM 5433) **f** *C. osseus* (dbM 5677) **g** *C. ivanovi* sp. nov. (dbM 5491) (**ps** = posterior surface of propodeum **fp** = postero-medial flange of propodeum **pp** = postero-lateral process **ll** = lateral lamella).

along medial margin adjoining sternum VI, thereby slightly but continuously diverging from lateral margin of tergum VI.

Metasomal sternum I shiny, finely shagreened, with tiny setae but without punctures. Sterna II–V posteriorly with broad stripe of asetose, translucent cuticula adjacent to posterior margin of more strongly sclerotized cuticula; small sparse row of setae along posterior sclerotized margin somewhat projecting over anterior part of translucent

stripe of cuticula; small outer area of postero-lateral corners distinctly depressed with some deep macropunctures; rest of sclerotized cuticula shiny, at least on anterior half of each sternum finely shagreened becoming weaker towards its posterior end; sternum II with median area moderately covered with small shallow macropunctures from which short pale setae arise, laterally sparsely covered with shallow macropunctures and micropunctures, micropunctation becoming fairly denser along posterior margin; sterna III–V anteriorly with moderate to dense shallow macropunctation, posteriorly changing into nearly unpunctured cuticula becoming moderately to densely covered by micropunctures further postero-laterally and along posterior margin. Posterior margin of sterna I–IV straight, posterior margin of sternum V medially concave running in a gentle curve. Sternum VI (Fig. 8c) tapering towards distal end; with outer margin forming bulged shiny rim, anteriorly raised to inwardly bent carina, postero-laterally strongly curved medially resulting in blunter appearance of distal end of sternum VI; rim at posterior end obtuse to nearly transverse, partly interrupted by depressions of macropunctures, postero-medially protruded into little median spine; cuticula with smooth median area tapering posteriorly, slightly raised to weak median keel at posterior end that continues into median spine, laterally with moderately spaced deep macropunctures becoming densely spaced and partly fused along lateral rim; stiff setae of moderate length arising obliquely backwards from macropunctures; posterior along distal end of rim densely covered with posteriorly directed stiff setae medially of same length as median spine becoming shorter anteriorly; at dorso-posterior margin dorsal (inner) cuticula protruded into irregularly serrated crystalline horizontal lamella situated immediately above the posteriorly directed stiff setae (Fig. 8h-i), dorso-medially fused with median spine, at postero-lateral edges somewhat more protruded.

Male. Colour (Fig. 2): Resembles female, except as follows. Light yellowish-white are: large M-shaped band on frons, laterally filling each ocular sinus (Fig. 9b); clypeus except dorso-lateral vertical sides and brownish translucent ventro-medial margin; little spot proximally on outside of mandible; complete longitudinal stripe on outside of fore-tibia; whole outside of mid- and hind-tibia; outside of hind-metatarsus. Labrum translucent brown with two yellowish-white antero-lateral spots medially fused. Terga II–VI with laterally and medially widened posterior band, anteriorly with small brownish tinge towards adjacent blackish-brown area, on terga III–VI interrupted on each side of middle by blackish-brown area. Tergum VII blackish-brown. Antenna black, with light yellowish-white stripe antero-medial on A3–A7 and proximal part of A8.

Structure: Resembles female, except as follows. Head in front view 1.49 times as wide as long (Fig. 9b, i). Mandible with single pointed tooth at distal end and two smaller acute teeth distally on antero-medial margin. Labrum with flat ventro-median area, shiny with few thin short pale setae; dorsal and lateral area set off by tiny edge, strongly convex, weakly shagreened with rows of micropunctures from which short thin pale setae arise. Clypeus 1.36 times wider than long, strongly convex; shiny, ventro-medial area above emargination smooth, sparsely covered with micropunctures, dorsally and laterally changing into moderately spaced micro- and dense uneven shallow macropunctation; covered with short fine pale erected setae with distal end not

Figure 8. a–c Female sternum VI in ventral view **a** *C. yemenensis* (dbM 4759) **b** *C. ivanovi* sp. nov. (dbM 5491) **c** *C. cagrii* sp. nov. (dbM 5611) **d–f** female fore femur in posterior view **d** *C. cyprius* (dbM 5431) **e** *C. osseus* (dbM 5678) **f** *C. ivanovi* sp. nov. (dbM 5493) **g–i** female sternum VI posterior margin in dorso-posterior view **g** *C. ivanovi* sp. nov. (dbM 5493) **h** *C. cagrii* sp. nov. (dbM 5607) **i** *C. cagrii* sp. nov. (dbM 5618).

curved. Frons with distinct depression dorsal to protruding centre of supra-antennal area. Antennal club formed by A8–A12 in dorsal view about 1.68 times as long as broad; asymmetrical (Fig. 9g), with anterior margin evenly rounded, strongly curved

at distal end into straight-line transverse distal margin, and posterior margin nearly straight, bent into distal margin at postero-distal edge forming nearly right angle; with distinct longitudinal depression on posterior two-fifth of ventral side bearing three somewhat oval shaped tyloids, situated within A9, A10 and A11, tyloid of A9 smaller than others. Mid-coxa without small spine at distal end on anterior side close to anterior-medial angle.

Tergum VII at posterior end with narrow median lobe and well set off postero-lateral angle on each side (Fig. 9e); median lobe moderately produced, its posterior margin weakly concave in middle, with adjacent posterior translucent lamella fairly emarginated; translucent lamella continues on ventral side (in ventral view) at its base on both sides into distinct carina running anteriorly along medial margin adjoining sternum VII+VIII (fused); medial margin of postero-lateral angles running in semi-circular curve medially continuing into cuticula of median lobe slightly dorsal to base of translucent lamella; posterior median lobe and postero-lateral angles nearly horizontal distinctly set off at their base by sharp bend from anteriorly adjacent rising part of tergum; posteriorly with increasingly close and deep macropunctation, strongest medially above sharp bend; interstices anteriorly distinctly shagreened, posteriorly smooth and more shiny, postero-medially moderately covered with tiny pale setae.

Sternum VIII (Fig. 14f) acutely produced running into two pointed lancet-like tips at posterior end with deep median incision between them, lancet-like tips and median incision between them narrower than in *C. ivanovi* sp. nov.; convex with large longitudinal depression in centre, lateral margins in proximal half bent horizontally; cuticula shiny, with shallow macropunctures; pale postero-medially directed setae arising from macropunctures, posteriorly increasing in length, forming little tuft projecting over posterior median incision. Sparse transverse fringe of tiny setae along distal end of sternum VII projecting over base of fused sternum VIII.

Male genital as in Figs 10f, 11f, 12f, 13f. Genital comparatively narrow and elongated; in lateral view broadest at base of stipites tapering into flat distal ends of harpides, in dorsal view basal opening narrow with stipites curved towards cupula without substantial lateral enlargement. Dorsal part of stipes distally continuing into harpide, with dorsal outline of harpide nearly straight in lateral view. Harpide in ventral view with tapering spatula-like distal end with distinctly concave latero-distal margin; medial margin strongly bent in ventral direction resulting in longitudinal vertical duplication, upper margin of which slightly curved towards longitudinal axis of harpide in addition; ventro-lateral margin continues proximally into curved sides of stipes; distally moderately covered with thin setae, with longest setae along apical margin. Volsella continues ventro-proximally into ventral plate of stipes; medially set off from ventral plate of stipes by deep emargination of medial margin; ventrally moderately covered with strong setae that are longer apically; apically on dorsal side with strongly sclerotized large, dark tubercles. Aedoeagus with broadly rounded distal end; thyrsoi not distinctly separated from surrounding transparent soft cuticula, though clearly stronger sclerotized laterally along basal two-third of aedoeagus, only weakly converging towards distal end; each thyrsos ventrally with distinct ventro-anteriorly directed comparatively broad and blunt process (uncus thyrsos); apodema thyrsos

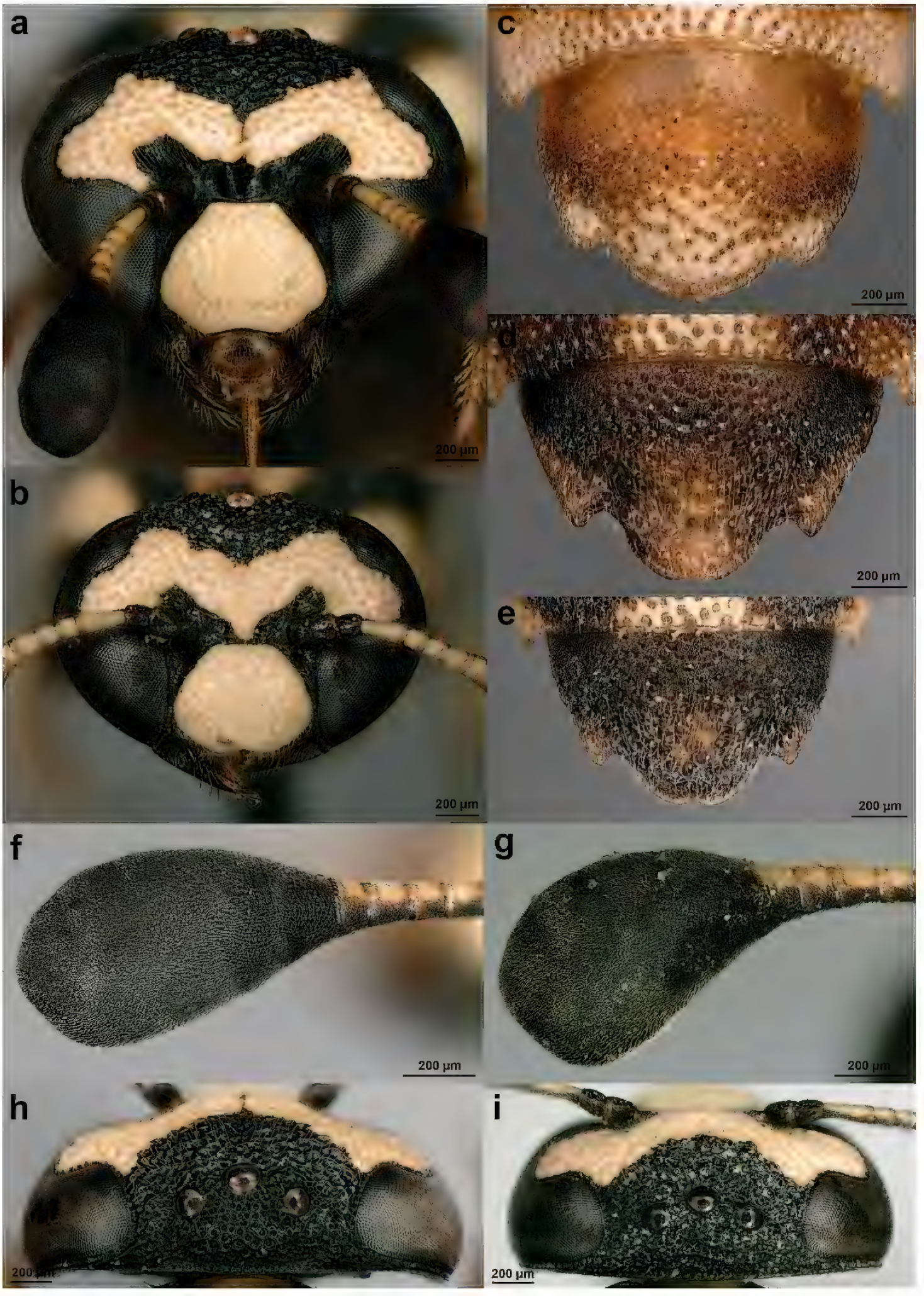

Figure 9. a, b Male head in frontal view **a** *C. ivanovi* sp. nov. (dbM 5498) **b** *C. cagrii* sp. nov. (dbM 5619) **c–e** male tergum VII in dorso-posterior view **c** *C. osseus* (dbM 5521) **d** *C. ivanovi* sp. nov. (dbM 5498) **e** *C. cagrii* sp. nov. (dbM 5619) **f, g** male antennal club in dorsal view **f** *C. ivanovi* sp. nov. (dbM 5499) **g** *C. cagrii* sp. nov. (dbM 5619) **h, i** male head in dorsal view **h** *C. ivanovi* sp. nov. (dbM 5498) **i** *C. cagrii* sp. nov. (dbM 5619).

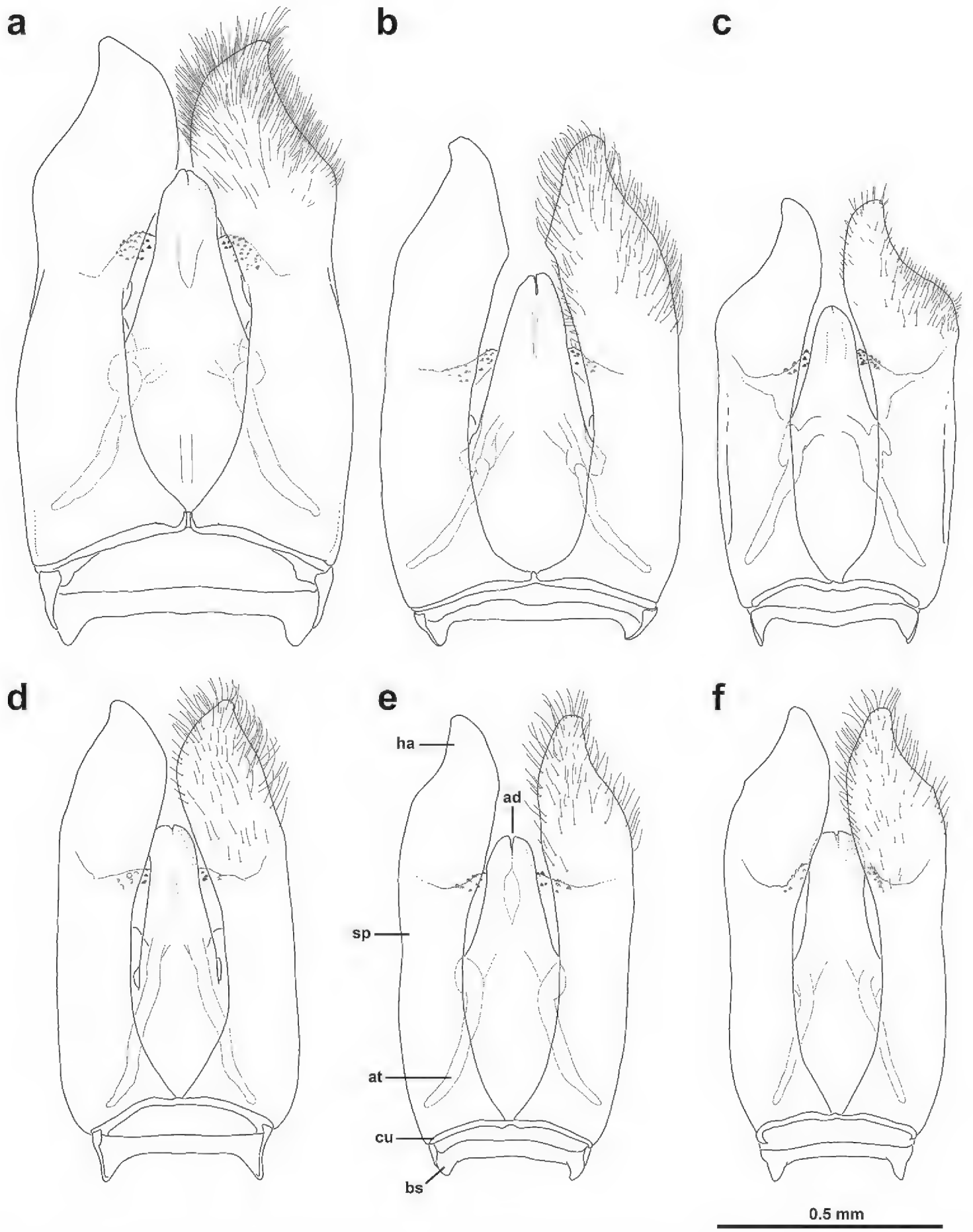

Figure 10. Male genitalia in dorsal view **a** *C. rugiceps* (dbM 2834) **b** *C. cyprius* (dbM 5452) **c** *C. yemenensis* (dbM 5531) **d** *C. osseus* (dbM 5521) **e** *C. ivanovi* sp. nov. (dbM 5497) **f** *C. cagrii* sp. nov. (dbM 5619) (**ad** = aedoeagus **at** = apodema thyrsos **bs** = basal sclerite **cu** = cupula **ha** = harpide **sp** = stipes).

delicate, anteriorly running nearly straight. Basal region with cupula and basal sclerite; cupula fused with base of each stipes connecting both stipites dorsally, while ventromedial ends of cupula are separated by wide gap from each other; basal sclerite forming

half ring on ventral side basal to cupula; medially slightly convex in ventral direction, laterally strongly curved upwards forming vertical sides, rounded at dorsal end.

Measurements. Measurements of the exoskeleton are listed in Table 1.

DNA barcoding. COI-5P gene sequences were obtained from two specimens and entered in BOLD database (CECYP005-20, CECYP006-20). The intraspecific sequence divergence of *C. cagrii* sp. nov. is 0.37%. The clade is clearly separated from the other investigated *Celonites* taxa (Fig. 16). The lowest interspecific genetic distance exists between *C. cagrii* sp. nov. and *C. ivanovi* sp. nov. with a minimum of 6.86% (mean 7.40%).

Etymology. The species is named after M. Çağrı Yildirim, the son of E. Yildirim.

Distribution. Turkey, Armenia (Fig. 17).

Bionomics. Habitat. The locus typicus of *C. cagrii* sp. nov. is situated in an arid mountainous area at an altitude of 1275 m a.s.l. in a valley near Akşar, which is a village in the Şenkaya district of Erzurum. Mean annual temperature is approximately 7.2 °C, annual precipitation is 456 mm (calculated by https://de.climate-data.org). The sides of the valley are formed by the steep slopes of adjacent dry mountains and a stream is running at its bottom. The upper part of the valley is covered with rocks, while the lower part is characterized by stony ruderal sites mainly used for grazing, and a few dry pastures and fields (Fig. 18i). General plant diversity is low, but plants of *Heliotropium ellipticum* Ledeb. (Boraginaceae) were growing solitarily or in patches on the sides of a little dirt road in an area that extended over 300 m, where the imagines of *C. cagrii* sp. nov. were observed.

Flower association. Twelve females and a single male of *C. cagrii* sp. nov. were collected while they were visiting flowers of *Heliotropium ellipticum*.

Celonites ivanovi Mauss & Fateryga, sp. nov.

http://zoobank.org/1AB3C8D3-A445-409F-8443-C3BC920350B8

Holotype. ♀ (dbM 5492), "[Russia] Dagestan, Maydanskoye 42°36'16"N 46°58'10"E [corrected to 42°36'07"N, 46°58'13"E in 2021] 11.VI.2019 on *Heliotropium styligerum* leg. [A.V.] Fateryga" OLML (Figs 5e, 6c).

Paratypes. "[Russia] Dagestan, Untsukulskiy distr. vicinity of Maydanskoye [42°37'36"N 46°56'48"E] on *Heliotropium styligerum* 23.06.2018 leg. [A.V.] Fateryga", 1♀ AF, 1♀ (dbM 5287) VM; "[Russia] Dagestan Maydanskoye 42°36'16"N 46°58'10"E [corrected to 42°36'07"N, 46°58'13"E in 2021] 11.VI.2019 leg. [A.V.] Fateryga", 1♂ (dbM 5497) AMNH, 1♂ (dbM 5498) OLML, 1♂ ZISP, 3♂ AF, 2♂ (dbM 5496, 5499) VM; "[Russia] Dagestan, Maydanskoye 42°36'16"N 46°58'10"E [corrected to 42°36'07"N, 46°58'13"E in 2021] 11.VI.2019 on *Heliotropium styligerum* leg. [A.V.] Fateryga", 1♀ (dbM 5494) AMNH, 1♀ ZISP, 5♀ AF, 3♀ (dbM 5490, 5491, 5493) 1♂ (dbM 5495) VM; "[Russia] Dagestan, Maydanskoye 42°36'07"N, 46°58'13"E 15.VI.2021 on *Heliotropium styligerum* leg. [A.V.] Fateryga", 4♀ (dbM 5856, 5857, 5858, 5995) VM; "[Russia] Dagestan, Maydanskoye 42°36'07"N, 46°58'13"E 16.VI.2021 on

Table 1. Measurements of the exoskeleton of females and males of *Celonites cagrii* sp. nov., *C. ivanovi* sp. nov., *C. osseus and C. clarus* (x = median; min = minimum, max = maximum, n = sample size; maximum accuracy 0.011 mm, all distances in mm).

Genus	female																male									
Species	*C. cagrii* sp. nov.				*C. ivanovi* sp. nov.				*C. osseus*				*C. clarus*				*C. cagrii* sp. nov.				*C. ivanovi* sp. nov.				*C. osseus*	
Parameter	x	min	max	n	x	min	max	n	x	min	max	n	x	min	max	n	x	min	max	n	x	min	max	n	x	n
lateral ocelli distance	**0.39**	0.36	0.42	13	**0.41**	0.37	0.43	11	**0.39**	0.36	0.43	10	**0.41**	0.36	0.42	3	**0.34**	0.34	0.35	3	**0.39**	0.32	0.43	5	**0.39**	1
med./lat. ocellus distance	**0.13**	0.12	0.14	13	**0.14**	0.13	0.17	11	**0.14**	0.12	0.15	10	**0.14**	0.12	0.14	3	**0.11**	0.11	0.12	3	**0.13**	0.10	0.14	5	**0.13**	1
compound eyes distance	**1.17**	1.11	1.22	13	**1.21**	1.16	1.24	11	**1.17**	1.12	1.24	10	**1.21**	1.16	1.22	3	**0.90**	0.86	0.94	3	**0.86**	0.72	1.09	5	**1.09**	1
A1 length	**0.17**	0.15	0.18	13	**0.19**	0.18	0.20	11	**0.17**	0.15	0.18	10	**0.15**	0.14	0.17	3	**0.17**	0.15	0.19	3	**0.19**	0.17	0.20	5	**0.17**	1
A3 length	**0.23**	0.22	0.24	13	**0.24**	0.23	0.25	11	**0.23**	0.21	0.24	10	**0.18**	0.18	0.19	3	**0.23**	0.23	0.26	3	**0.24**	0.23	0.26	5	**0.22**	1
A3 width	**0.09**	0.08	0.10	13	**0.10**	0.09	0.11	11	**0.09**	0.09	0.10	10	**0.09**	0.09	0.10	3	**0.10**	0.10	0.10	3	**0.11**	0.09	0.11	5	**0.11**	1
A4–A5 length	**0.17**	0.15	0.18	13	**0.18**	0.15	0.18	11	**0.17**	0.15	0.18	10	**0.13**	0.12	0.14	3	**0.20**	0.19	0.22	3	**0.20**	0.18	0.21	5	**0.21**	1
A8–A12 length	**0.65**	0.63	0.67	13	**0.70**	0.66	0.74	11	**0.69**	0.65	0.72	10	**0.64**	0.62	0.70	3	**0.85**	0.81	0.88	3	**0.85**	0.78	0.95	5	**0.99**	1
A8–A12 width	**0.31**	0.29	0.32	13	**0.32**	0.31	0.34	11	**0.32**	0.32	0.34	10	**0.32**	0.31	0.34	3	**0.48**	0.47	0.48	3	**0.44**	0.42	0.51	5	**0.45**	1
antennal sockets distance	**0.56**	0.54	0.59	13	**0.58**	0.54	0.61	11	**0.58**	0.54	0.61	10	**0.57**	0.54	0.63	3	**0.41**	0.40	0.42	3	**0.42**	0.40	0.48	5	**0.47**	1
clypeus max. width	**0.87**	0.85	0.90	13	**0.94**	0.87	0.97	11	**0.90**	0.88	0.95	10	**0.88**	0.86	0.92	3	**0.70**	0.68	0.73	3	**0.70**	0.67	0.84	5	**0.77**	1
clypeus apical width	**0.46**	0.43	0.51	13	**0.54**	0.44	0.56	11	**0.46**	0.40	0.48	10	**0.41**	0.31	0.44	3	**0.34**	0.33	0.37	3	**0.45**	0.33	0.50	5	**0.39**	1
clypeus length	**0.62**	0.59	0.65	13	**0.68**	0.65	0.70	11	**0.65**	0.62	0.69	10	**0.58**	0.56	0.61	3	**0.53**	0.52	0.55	3	**0.56**	0.50	0.64	5	**0.58**	1
mesonotum width	**2.10**	1.99	2.18	13	**2.30**	2.13	2.38	11	**2.21**	2.10	2.27	10	**2.04**	1.93	2.13	3	**1.90**	1.88	2.02	3	**2.24**	1.85	3.77	5	**2.18**	1
mesoscutum length	**1.31**	1.24	1.38	13	**1.48**	1.39	1.53	11	**1.42**	1.29	1.50	10	**1.33**	1.29	1.39	3	**1.12**	1.03	1.19	3	**1.12**	1.00	1.34	5	**1.24**	1
wing length	**4.14**	4.00	4.32	13	**4.69**	4.46	4.90	11	**4.53**	4.23	4.65	10	**4.09**	4.00	4.32	3	**3.96**	3.77	4.09	3	**4.14**	3.77	4.62	5	**4.37**	1
R+Sc length	**2.21**	2.18	2.32	13	**2.49**	2.41	2.58	11	**2.44**	2.24	2.55	10	**2.16**	2.13	2.35	3	**2.13**	2.04	2.21	3	**2.16**	2.04	2.60	5	**2.32**	1
number of hamuli	**7**	6	8	13	**7**	6	8	11	**7**	7	9	10	**7**	7	9	3	**8**	7	9	3	**7**	7	8	5	**8**	1
femur I length	**1.01**	0.97	1.06	13	**1.11**	1.08	1.14	10	**1.04**	0.94	1.10	10	**0.97**	0.95	0.99	3	**0.90**	0.84	0.95	3	**1.00**	0.87	1.07	4	**0.95**	1
tibia I length	**0.67**	0.62	0.69	13	**0.76**	0.74	0.77	11	**0.69**	0.66	0.74	10	**0.64**	0.63	0.65	3	**0.62**	0.62	0.65	3	**0.67**	0.62	0.75	5	**0.64**	1
tibia I width	**0.36**	0.34	0.40	13	**0.42**	0.40	0.45	11	**0.20**	0.19	0.20	10	**0.36**	0.36	0.40	3	**0.17**	0.17	0.17	3	**0.33**	0.29	0.36	5	**0.34**	1
metatarsus I length	**0.45**	0.40	0.48	13	**0.51**	0.46	0.54	11	**0.42**	0.39	0.43	10	**0.45**	0.43	0.51	3	**0.28**	0.28	0.29	3	**0.45**	0.42	0.48	5	**0.51**	1
metatarsus I width	**0.19**	0.18	0.20	13	**0.20**	0.19	0.21	11	**0.13**	0.13	0.14	10	**0.18**	0.18	0.20	3	**0.10**	0.10	0.10	3	**0.17**	0.14	0.19	5	**0.19**	1
tarsus I T2–T5 length	**0.14**	0.13	0.14	13	**0.15**	0.13	0.15	11	**0.50**	0.47	0.54	10	**0.12**	0.12	0.13	3	**0.42**	0.40	0.45	3	**0.11**	0.10	0.12	5	**0.11**	1
tergum I width	**2.21**	2.10	2.30	13	**2.41**	2.30	2.49	11	**2.30**	2.13	2.46	10	**2.10**	2.07	2.27	3	**2.07**	2.04	2.27	3	**2.27**	1.90	2.52	5	**2.30**	1
tergum I length	**0.88**	0.73	0.94	13	**1.02**	0.95	1.04	11	**0.94**	0.87	1.04	10	**0.87**	0.78	0.90	3	**0.88**	0.80	0.96	3	**0.97**	0.80	1.12	5	**1.00**	1
tergum II width	**2.18**	2.07	2.24	13	**2.41**	2.27	2.52	11	**2.32**	2.21	2.46	10	**2.07**	2.07	2.30	3	**2.07**	1.99	2.18	3	**2.24**	1.96	2.52	5	**2.35**	1
total length	**5.7**	5.3	6.6	13	**6.0**	5.6	6.5	11	**6.1**	5.4	6.2	10	**5.4**	5.3	6.5	3	**5.4**	5.3	5.4	2	**6.2**	5.0	7.0	4	**6.5**	1

Heliotropium styligerum leg. [A.V.] Fateryga", 2♀ (dbM 5859, 5860) VM; "[Russia] Dagestan, Maydanskoye 42°36'07"N, 46°58'13"E 16.VI.2021 leg. [A.V.] Fateryga", 1♂ (dbM 5996) VM; "[Russia] Dagestan, vicinity of Turtsi 42°11'34"N, 47°09'33"E on *Heliotropium styligerum* 22.VI.2021 leg. [A.V.] Fateryga", 1♀ (dbM 5997) VM.

Diagnosis. See key.

Description. Female. Colour (Figs 2, 4e): Black. The following are yellowish-white: large rectangular spot dorso-medial on clypeus; two small spots adjoining ventral margin of clypeus to both sides of median emargination; small spot on each ocular sinus and two spots on frons; medium-sized spot on antero-dorsal angle of pronotum (humeral spot); broad stripe along dorso-medial (inner) margin of pronotum, anteriorly somewhat angularly enlarged with little median dent; large spot on dorsal mesepisternum; laterally directed process of axilla; medium-sized spot postero-medially on scutellum; dorsal and ventral side of propodeal lamella; antero-lateral one-fifth and posterior two-fifth of tegula, interrupted by brownish translucent area on bulge changing into black towards antero-medial margin of tegula; posterior band on tergum I occupying whole of sides but less than half of middle part, somewhat widened anteriorly in median axis, anteriorly with small brownish tinge towards adjacent black area; laterally and medially widened posterior bands on terga II–V, anteriorly with small brownish tinge towards adjacent black area, interrupted on each side of middle by brownish area (Fig. 6b); little longitudinal spot antero-medial on tergum VI; small spots on postero-lateral edges of sterna II–III; outside of distal tips of fore-, mid- and hind-femora; outside of proximal end of fore-tibia; outside of mid-tibia except small diagonal blackish-brown interruption in middle; outside of hind-tibia except blackish ring covering one-third below middle. Brown are: distal half of mandible; maxillary and labial palpi, protrudeable parts of proboscis; ventral margin of labrum; translucent ventro-medial margin of clypeus; postero-lateral margin of scutellum; median third of metanotum; postero-lateral process of propodeum; humeral plate (at base of wing underneath tegula); sides and posterior translucent margin of tergum VI; tarsi; sternum I; sterna II–V, lighter along posterior translucent margin. Antenna black except: weak yellowish markings medial on A4–A6; brown-suffused area ventral on A9–A11 and proximal part of A12. Wings moderately infuscate, pterostigma black, veins black becoming somewhat lighter at base.

Variation (number of specimens in brackets): Yellowish-white markings: clypeus with two additional lateral spots (1), only with two small separate spots dorso-medial on clypeus (1) or clypeus completely black (1); spot on ocular sinus and frons narrowly fused (1); spot on ocular sinus or frons asymmetrically reduced (4) or completely reduced (1); short narrow spot on gena along postocular carina at dorso-lateral corner of head (3); humeral spot small (4); little spot antero-ventrally on mesepimeron (1); little spot postero-medially on mesoscutum (5); bands on terga II–V interrupted on each side of middle by blackish-brown area (3); antero-medial spot on tergum VI absent (2); continuous stripe on outside of mid-tibia (5); continuous stripe on outside of hind-tibia (2) or marking on outside of mid- and hind-tibia reduced to small area at distal and proximal end (3); little spot disto-medially on A3 (1), weak yellowish markings medial on A7 (3).

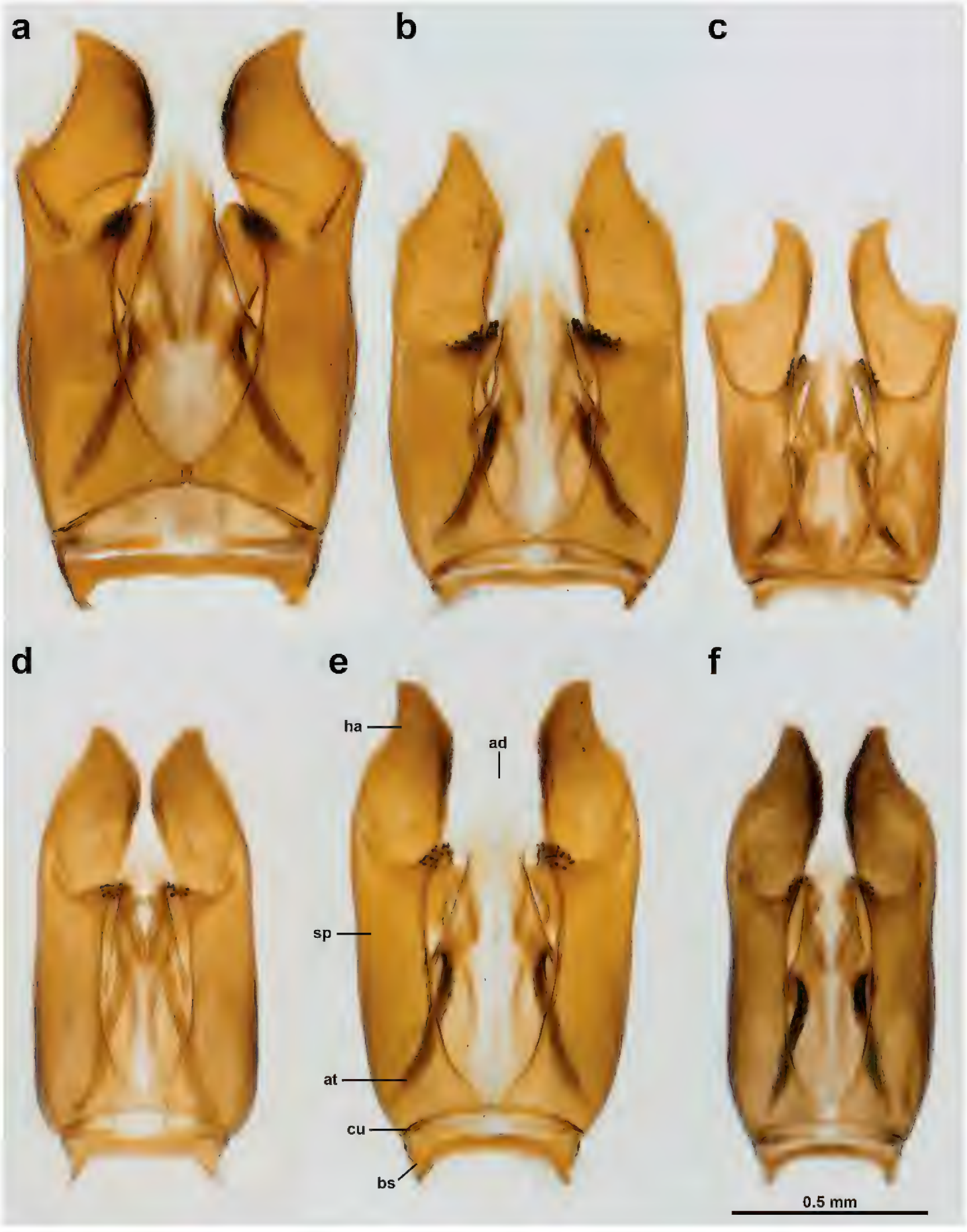

Figure 11. Microphotos of male genitalia in dorsal view **a** *C. rugiceps* (dbM 5450) **b** *C. cyprius* (dbM 5439) **c** *C. yemenensis* (dbM 5532) **d** *C. osseus* (dbM 5521) **e** *C. ivanovi* sp. nov. (dbM 5498) **f** *C. cagrii* sp. nov. (dbM 5619) (**ad** = aedoeagus **at** = apodema thyrsos **bs** = basal sclerite **cu** = cupula **ha** = harpide **sp** = stipes).

Structure: Head in front view 1.48 times as wide as long in median (min 1.45, max 1.53, n=5) (Fig. 4e). Mandible with two large blunt incisivi at distal end separated by acute-angled cleft and two smaller more acute subapical incisivi on antero-medial

margin. External side of mandible (Fig. 5d) distally bearing longitudinal rows of long stiff setae; at base without distinct transverse depression; basal area with shagreened cuticula moderately covered with pubescence of tiny thin setae (longer than in *C. cyprius*); anterior to condylar ridge cuticula of basal area extends further apically becoming distinctly striated in longitudinal direction; this area contrasts to smooth shiny cuticula on condylar ridge and postero-apically adjoining surface; condylar ridge distinct at basal two-third of mandible continuing in more angled curve into apical side (strongest bend approximately after basal third of mandible). Labrum matt shining, finely shagreened and longitudinally wrinkled; densely covered with pale stiff setae directing obliquely downwards; setae as long as A7 maximum wide, with distal end curved ventro-medially, laterally at apex of labrum thicker with larger diameter at base. Clypeus 1.4 times wider than long (Fig. 5b); translucent ventro-medial margin becoming much narrower medially resulting in distinct median emargination; cuticula shiny, ventro-medial above emargination with sparse micropunctation becoming moderately spaced dorsally and laterally on disc with larger irregular flat depressions and wrinkles in addition; dorso-lateral vertical parts of clypeus smooth with moderately spaced micropunctation partly striated at base; covered with pale thin stiff setae arising from micropunctures; setae on disc about as long as A4, vertically erected with distal ends strongly curved in ventro-medial direction, on sides shorter lying more flatly. Frons very coarsely punctured, interstices shining, raised to ±transversal little rounded ridges; protruding central part of supra-antennal area smooth without punctures in middle; semi-circular depression of antennal groove wrinkly shagreened; slight median depression dorsal to supra-antennal area, frontal line weak; sparsely covered with pale short setae arising from coarse punctures, setae on supra-antennal area as on clypeus. Vertex with close macropunctation, becoming more closely reticulate behind ocelli with smaller punctures and interstices more strongly raised forming short sharp-edged ±transversal ridges; sparsely covered with pale short setae arising from punctures; cuticula of interstices shiny, weakly shagreened (Fig. 5e). Median ocellus 1.2 times larger in diameter than lateral ocelli; median ocellus somewhat bilateral symmetric with anterior sector less strongly curved than posterior sector; lateral ocelli ±circular (in dorso-lateral view). Compound eyes sparsely covered with tiny setae. Preoccipital carina (*sensu* Snelling 1986) sharp; medially straight, nearly transversal; laterally behind dorso-lateral end of each compound eye curved downwards for short distance becoming obsolete posterior to dorsal end of postocular carina (*sensu* Snelling 1986). Gena narrow, less than half as wide as basal width of A3. Postocular carina sharp; extends dorsad from posterior mandibular articulation along posterior margin of gena; ends level with dorsal end of compound eye anterior to preoccipital carina that runs parallel for short distance. Antennal articles A8–A12 forming ventrally flattened club about 2.1–2.3 times as long as broad (in dorsal view).

Pronotum with anterior margin raised to carina; anterior pronotal carina (*sensu* Carpenter 1988) in antero-ventral area of pronotum starting close to posterior margin, running in a short parabolic curve antero-laterally and then parallel to posterior margin, preceding distinct crenate groove; fairly projecting in posterior direction over anterior border of crenate groove, especially along ventral parabolic curve; crenate

groove with anterior wall nearly vertical, bottom with sulcature of transverse ribs, posteriorly gradually inclined up to posterior margin of pronotum, cuticula in this area obliquely striated with some folds ±continuing into bottom ribs; on lateral quarter distinct posterior pronotal carina sharply separating semicircular antero-ventral area

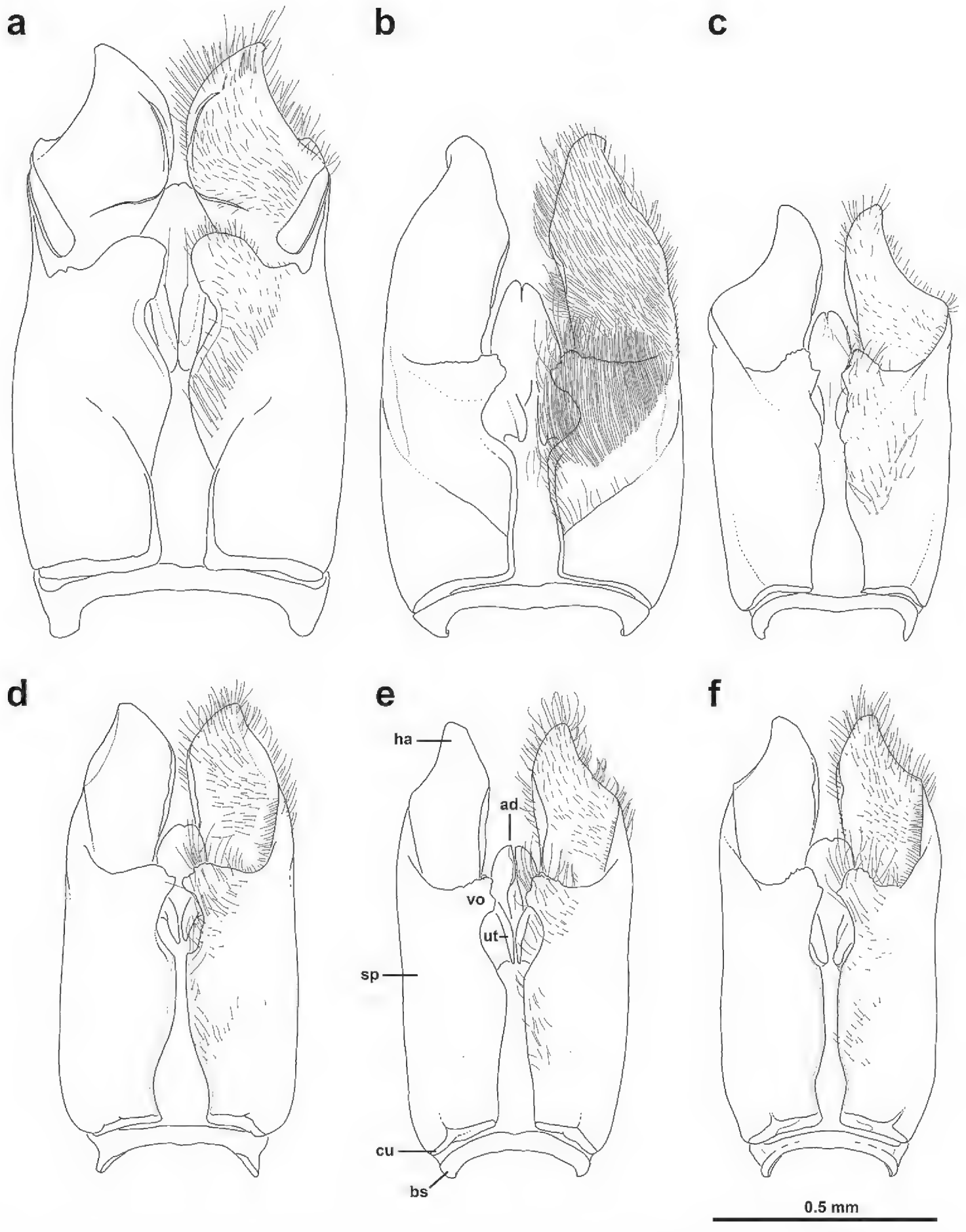

Figure 12. Male genitalia in ventral view **a** *C. rugiceps* (dbM 2834) **b** *C. cyprius* (dbM 5452) **c** *C. yemenensis* (dbM 5531) **d** *C. osseus* (dbM 5521) **e** *C. ivanovi* sp. nov. (dbM 5497) **f** *C. cagrii* sp. nov. (dbM 5619) (**ad** = aedoeagus **bs** = basal sclerite **cu** = cupula **ha** = harpide **sp** = stipes **vo** = volsella **ut** = uncus thyrsos).

from dorsal area of pronotum; antero-medial front behind head nearly vertical; slight depression along dorso-medial margin especially anteriorly; posterior margin raised to short translucent carina dorsally in front of upper half of tegula; cuticula of antero-ventral area shiny, shagreened, with moderately spaced small shallow punctures; cuticula of dorso-lateral area shiny, with close coarsely reticulate macropunctation, smooth interstices raised to sharp edges postero-laterally forming lines; cuticula of pronotal lobe and dorsally continuing concavely curved depression in front of tegula smooth with a few distinct punctures but without reticulation, distinctly set off from adjacent parts of pronotum. Mesoscutum with distinct median notal suture on anterior third; cuticula shiny, coarsely reticulate with close deep macropunctation and narrow distinctly raised interstices (Fig. 6c). Mesoscutellum with distinct transverse sulcature of longitudinal cuticula-ribs separated by intercostal spaces along antero-medial margin; laterally with distinct smooth carina along posterior margin, carina medially increasingly reduced so that cuticula of medial lobe continues evenly into crenulate margin; cuticula more coarsely reticulate than on mesoscutum. Metanotum laterally with distinct sulcature of longitudinal cuticula-ribs separated by intercostal spaces; carina along posterior margin medially with small irregular indentations continuing in vertical median keel. Axilla produced into curved tapering projection which fits into slight emargination of tegula. Tegula shiny, closely covered by macropunctures except completely smooth central convex area. Antero-ventral parts of pronotum, ventral corner of dorsal mesepisternum (= prepectus *sensu* Richards 1962) and ventral mesepisternum form continuous antero-ventral cavity delimited from lateral parts of mesosoma by posterior pronotal carina, carina along ventral margin of dorsal mesepisternum and epicnemial carina. Dorsal mesepisternum separated from ventral mesepisternum by weak mesepisternal groove; with distinct carina along ventral margin, which is in one line with epicnemial carina though separated from it by little notch. Ventral mesepisternum with pronounced epicnemial carina, posteriorly deflexed backwards running medially in a curve to front of mid-coxa. Mesepimeron feebly separated by weak scrobal groove; postero-ventrally bearing mesopleural process (= process at or below mesepisternal scrobe *sensu* Richards 1962) of moderate size, distally rounded, its posterior side shagreened matt shiny without punctures. Cuticula laterally on mesopleurum and dorsal metapleurum shiny, with closely reticulate macropunctation; longitudinally striated by raised interstices in parts; ventral mesepisternum coarsely punctured with some interstices strongly raised to knife-like edges forming coarse rugose sculpture. Propodeum with horizontal propodeal triangles and dorso-lateral margins of posterior face of propodeum reduced to two pointed protuberances dorsally on each side of middle; posteriorly with narrow medial cuticula-fold running from dorsal margin to postero-medial flange of propodeum; posterior surface ventrally striated by strong vertical cuticula-folds arising below anterior transversal carina of postero-medial flange of propodeum, weakly coriaceous, with shallow macropunctures between folds, moderately covered with fine pale setae arising from macropunctures, laterally and dorsally continuing into coarsely reticulate macropunctation with shorter setae. Cuticula below lateral lamella shiny, on metepisternum densely horizontally wrinkled, on side of propodeum shagreened with moderately spaced small shallow punctures. Lateral lamella moderate, slightly

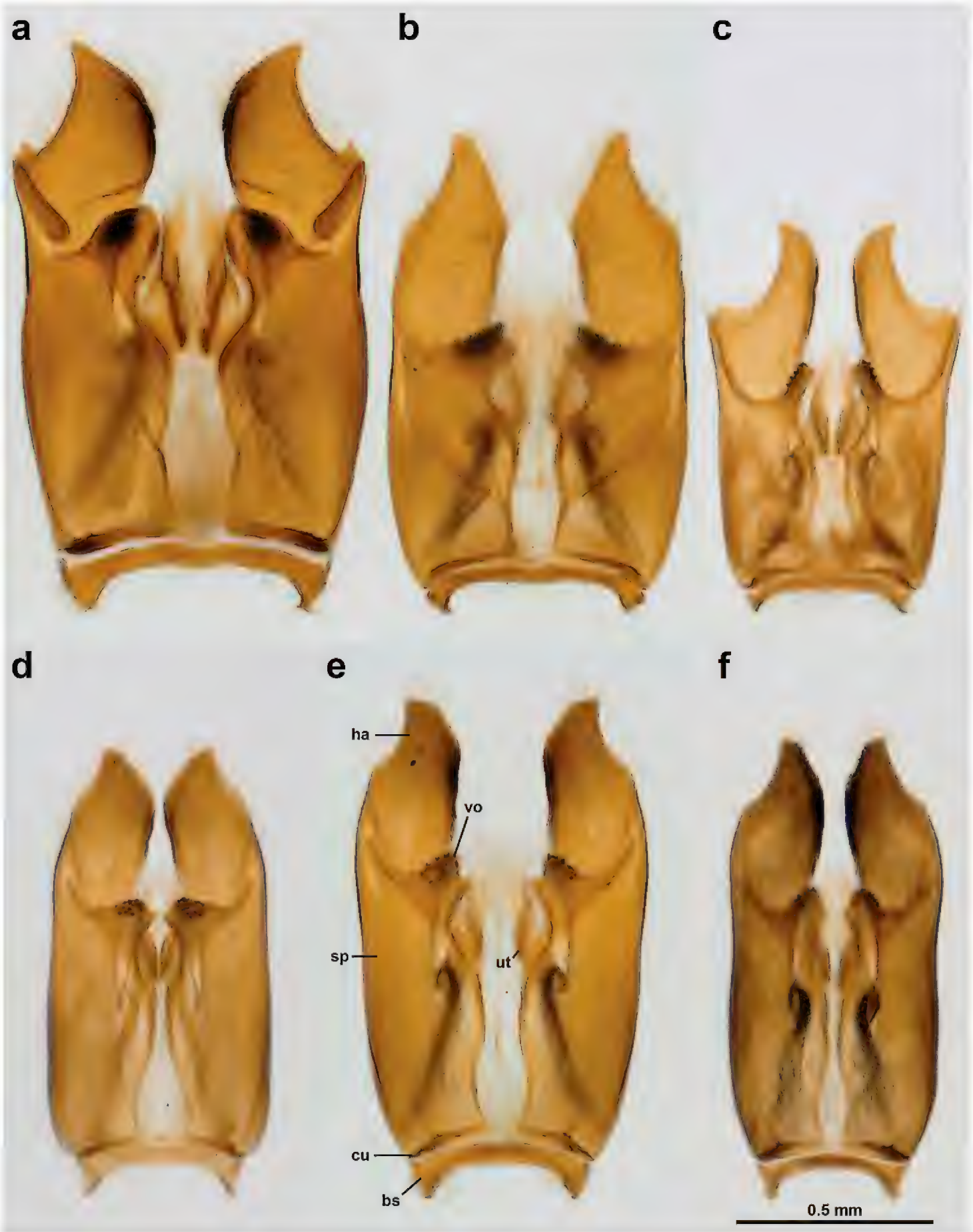

Figure 13. Microphotos of male genitalia in ventral view **a** *C. rugiceps* (dbM 5450) **b** *C. cyprius* (dbM 5439) **c** *C. yemenensis* (dbM 5532) **d** *C. osseus* (dbM 5521) **e** *C. ivanovi* sp. nov. (dbM 5498) **f** *C. cagrii* sp. nov. (dbM 5619) (**ad** = aedoeagus **bs** = basal sclerite **cu** = cupula **ha** = harpide **sp** = stipes **vo** = volsella **ut** = uncus thyrsos).

curved laterally downwards, its outer margin gently curved, its apex truncate, outer and posterior margins somewhat crenate; inner margin of lateral lamella and postero-lateral process of postero-medial flange of propodeum separated by moderate gap; anterior margin of postero-lateral process straight transverse, while posterior margin

converges in a gentle curve towards lateral apex; outline of emargination being broad at its base with short moderately wide neck between lateral apex of postero-lateral process and inner margin of lateral lamella and deep medially extended apical part (Fig. 7g); dorsal cuticula of lateral lamella and adjacent dorso-lateral part of propodeum shiny, with reticulate macropunctation. On whole exoskeleton single thin seta arises from bottom of each macropuncture, seta short if not stated otherwise.

Fore-femur postero-ventrally produced in middle forming anteriorly curved lobe (Fig. 8f) distally changing into tapering carina along ventral margin of femur; end of tibia when folded against femur coinciding with produced region; tarsomeres I–IV broad and flattened; underside of tibia and tarsomere I with strong obliquely distally directing setae forming stiff brush; underside of tarsomere I and II with comb-like row of particularly strong setae along distal margin. Claws ventrally with small tooth.

Metasomal terga with postero-lateral corners slightly produced; posterior margin of tergum I weakly crenulated, crenulation not produced into spines and not projecting over smooth translucent lower posterior margin of tergum; posterior margin of terga II–V weakly to moderately crenulated, crenulation in middle of terga II–IV produced into little slightly raised teeth projecting approximately to end of translucent lower posterior margin of terga (Fig. 6b); cuticula moderately shining, densely covered with reticulate macropunctation, punctures distinct, smaller and more regular than on mesoscutum; interstices finely shagreened. Tergum VI with lateral margins converging in weakly convex curve, at transition to posterior median lobe strongly bend inwards forming distinct postero-lateral angle on each side; posterior margin of posterior median lobe running in convex oval curve formed by distinct translucent lamella; posterior median lobe set off from more strongly sloping median area of tergum VI by slight concave curvature at its base; cuticula covered with fine pubescence of thin pale setae arising from micropunctures on interstices of reticulate macropunctation, slightly projecting beyond postero-median translucent lamella and lateral margins; on ventral side (viewed from ventral) posterior translucent lamella of median lobe continues on both sides into distinct carina running anteriorly along medial margin adjoining sternum VI, thereby slightly but continuously diverging from lateral margin of tergum VI.

Metasomal sternum I shiny, finely shagreened, with tiny setae but without punctures. Sterna II–V posteriorly with broad stripe of asetose, translucent cuticula adjacent to posterior margin of more strongly sclerotized cuticula; small sparse row of setae along posterior sclerotized margin somewhat projecting over anterior part of translucent stripe of cuticula; outer area of postero-lateral corners distinctly depressed, densely covered with macropunctures; rest of sclerotized cuticula shiny, finely shagreened on sterna II–III, shagreening weaker or missing on sternum IV and absent on sternum V; sternum II antero-laterally with moderately spaced shallow macropunctation and a few micropunctures becoming barely punctured towards posterior margin, whole medial area densely covered with small macropunctures from which short pale setae arise; sterna III–V anteriorly with moderate to dense shallow macropunctation, posteriorly changing into nearly unpunctured area along posterior margin. Posterior margin of sterna I–IV straight, posterior margin of sternum V medially concave running in a gentle curve. Sternum VI tapering towards distal end; with outer margin

Figure 14. Male fused sterna VII+VIII in ventral view **a** *C. rugiceps* (dbM 5289) **b** *C. cyprius* (dbM 5439) **c** *C. yemenensis* (dbM 5532) **d** *C. osseus* (dbM 5521) **e** *C. ivanovi* sp. nov. (dbM 5498) **f** *C. cagrii* sp. nov. (dbM 5619).

forming bulged rim, anteriorly raised to inwardly bent carina, posteriorly running in regular curve postero-medially protruded into little median spine (Fig. 8b); cuticula with smooth median area tapering posteriorly, slightly raised to weak median keel at posterior end that continues into median spine, laterally with moderately spaced deep macropunctures becoming densely spaced and partly fused along lateral rim; stiff setae of moderate length arising obliquely backwards from macropunctures; posterior along distal end of rim densely covered with posteriorly directed stiff setae medially of same length as median spine becoming shorter anteriorly; at dorso-posterior margin dorsal (inner) cuticula weakly protruded into horizontal lamella, situated immediately above the posteriorly directed stiff setae, dorso-medially slightly raised and fused with median spine, becoming continuously smaller postero-laterally (Fig. 8g).

Male. Colour (Fig. 2): Resembles female, except as follows. Yellowish-white are: large M-shaped band on frons, laterally nearly filling each ocular sinus except small area along upper inner margin of eye, narrowly interrupted medially on supra-antennal area; clypeus except dorso-lateral vertical sides and brownish translucent ventro-medial margin; complete longitudinal stripe on outside of fore-tibia; whole outside

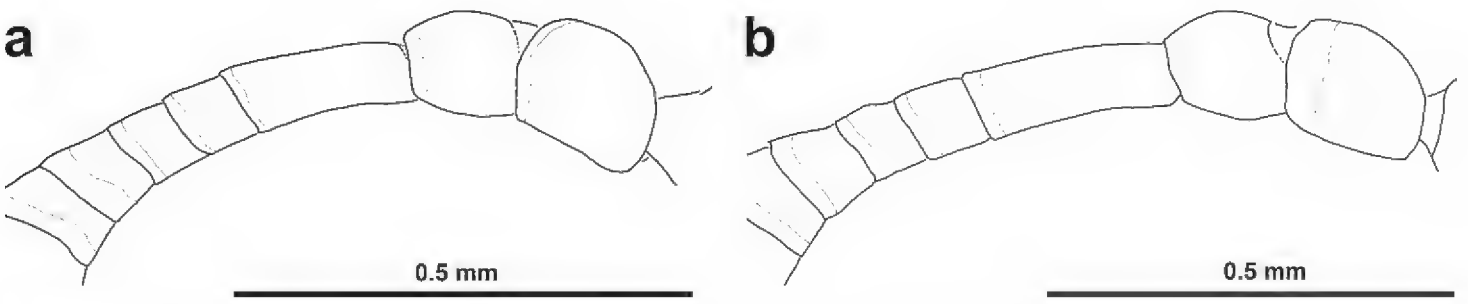

Figure 15. Female antennal articles A1–A6 in medial view (scaled to same size to show different proportions of A3) **a** *C. clarus* (dbM 5674) **b** *C. osseus* (dbM 5678).

of mid- and hind-tibia; outside of hind-metatarsus. Labrum translucent brown with two yellowish-white antero-lateral spots. Tergum VI as in terga II–V with laterally and medially widened posterior band, anteriorly with small brownish tinge towards adjacent black area, interrupted on each side of middle by brownish area. Tergum VII blackish-brown posteriorly changing into brown. Antenna black, with yellowish-white stripe antero-medial on A3–A7.

Variation (number of specimens in brackets): yellowish-white M-shaped band on frons filling ocular sinus completely (1), medially not completely interrupted (1); short narrow interrupted yellowish-white streak on gena along occipital carina at dorso-lateral corner of head (2); one or two little yellowish-white spots postero-medial on mesoscutum (2); humeral plate with yellowish-white marking (4); outside of mid-metatarsus yellowish-white (1).

Structure: Resembles female, except as follows. Head in front view 1.4–1.6 times as wide as long (Fig. 9a, h). Mandible with single pointed tooth at distal end and two smaller acute teeth distally on antero-medial margin. Labrum with flat ventro-median area, shiny with few thin short pale setae; dorsal and lateral area set off by tiny edge, strongly convex, weakly shagreened with rows of micropunctures from which short thin pale setae arise. Clypeus 1.3 times wider than long, strongly convex; shiny, ventro-medial area above emargination smooth, sparsely covered with micropunctures, dorsally and laterally changing into moderately spaced micro- and dense uneven shallow macropunctation; covered with fine pale erected setae, only very few with distally curved ends. Frons with distinct depression dorsal to protruding centre of supra-antennal area. Antennal club formed by A8–A12 about 1.8–1.9 times as long as broad (in dorsal view); asymmetrical (Fig. 9f), with anterior margin evenly rounded, strongly curved at distal end into weakly concave distal margin that is running obliquely upwards, and posterior margin weakly convex curved into distal margin at postero-distal edge forming blunt angle; with distinct longitudinal depression on posterior half of ventral side bearing three somewhat oval shaped tyloids, situated within A9, A10 and A11, tyloid of A9 smaller than others. Mid-coxa without small spine at distal end on anterior side close to anterior-medial angle.

Tergum VII at posterior end with characteristically narrow median lobe and well set off postero-lateral angle on each side (Fig. 9d); median lobe with translucent lamella, that continues on ventral side (in ventral view) at its base on both sides into distinct carina running anteriorly along medial margin adjoining sternum VII+VIII

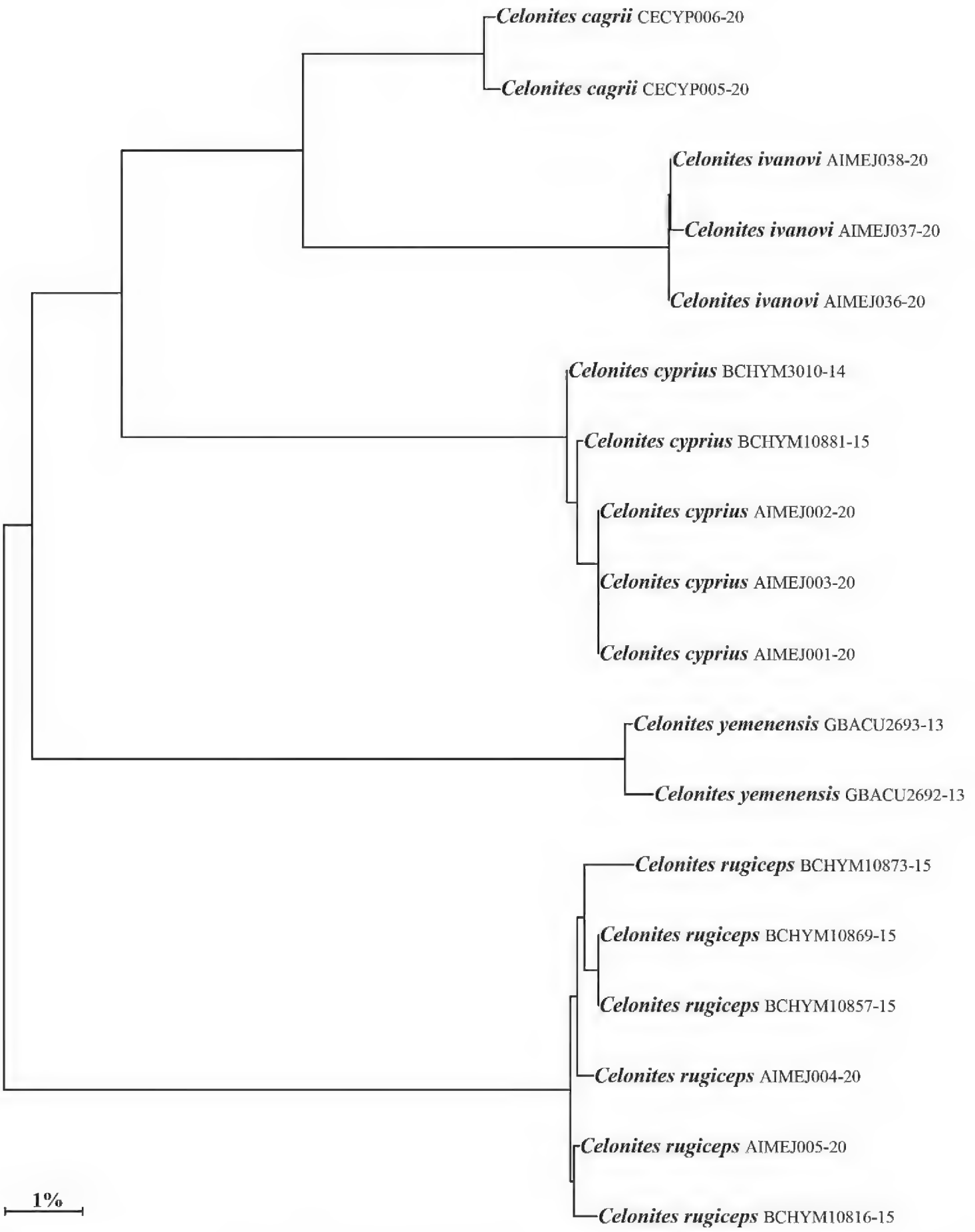

Figure 16. Neighbour joining BOLD taxon ID tree of 18 specimens of the *C. cyprius*-group based on COI-5P gene sequences (individually marked by BOLD process ID and assigned to species a priori by morphological characters; COI-5P gene sequence of *C. osseus* and *C. clarus* unknown).

(fused); medial margin of postero-lateral angles running in semi-circular curve medially continuing into cuticula of median lobe slightly dorsal to base of translucent lamella; posterior median lobe and postero-lateral angles nearly horizontal distinctly set off at their base by sharp bend from anteriorly adjacent rising part of tergum; posteriorly

with increasingly close and deep macropunctation, strongest medially above sharp bend; interstices anteriorly distinctly shagreened, posteriorly smooth and more shiny, postero-medially moderately covered with tiny pale setae.

Sternum VIII acutely produced running into two pointed lancet-like tips at posterior end with deep median incision between them (Fig. 14e); convex with large longitudinal oval depression in centre, lateral margins in proximal two-third bent horizontally; cuticula shiny, postero-medially with shallow macropunctures, becoming denser towards apical end; pale postero-medially directed setae arising from macropunctures, posteriorly increasing in length, forming little tuft projecting over posterior median incision. Sparse transverse fringe of tiny setae along distal end of fused sternum VII projecting over base of sternum VIII.

Male genital as in Figs 10e, 11e, 12e, 13e. Genital comparatively narrow and elongated; in lateral view broadest at base of stipites tapering into flat distal ends of harpides, in dorsal view basal opening narrow with stipites curved towards cupula without substantial lateral enlargement. Dorsal part of stipes distally continuing into harpide, with dorsal outline of harpide nearly straight in lateral view. Harpide in ventral view with tapering spatula-like distal end with distinctly concave latero-distal margin; medial margin strongly bent in ventral direction resulting in longitudinal vertical duplication, upper margin of which curved towards longitudinal axis of harpide in addition; ventro-lateral margin continues proximally into curved sides of stipes; distally moderately covered with thin setae, short on ventral side, dorsally longer with longest setae along apical margin. Volsella continues ventro-proximally into ventral plate of stipes; medially set off from ventral plate of stipes by deep emargination of medial margin; ventrally moderately covered with strong setae that are longer apically; apically on dorsal side with strongly sclerotized large, dark tubercles. Aedoeagus with narrowly rounded distal end; thyrsoi not distinctly separated from surrounding transparent soft cuticula, though clearly stronger sclerotized laterally along basal two-third of aedoeagus, converging towards distal end; each thyrsos ventrally with distinct ventro-anteriorly directed sharp process (uncus thyrsos); apodema thyrsos robust, anteriorly curved laterad. Basal region with cupula and basal sclerite; cupula fused with base of each stipes connecting both stipites dorsally, while ventro-medial ends of cupula are separated by wide gap from each other; basal sclerite forming half ring on ventral side basal to cupula; medially slightly convex in ventral direction, laterally strongly curved upwards forming vertical sides, rounded at dorsal end.

Measurements. Measurements of the exoskeleton are listed in Table 1.

DNA barcoding. COI-5P gene sequences were obtained from three specimens and entered in BOLD database (AIMEJ036-20, AIMEJ037-20, AIMEJ038-20). The intraspecific sequence divergence of *C. ivanovi* sp. nov. is low, reaching at most 0.18%. The clade is distinctly separated from the other investigated *Celonites* taxa (Fig. 16). The lowest interspecific genetic distance exists towards *C. cagrii* sp. nov. with a minimum of 6.86% (mean 7.40%).

Etymology. The species is named after Prof. Sergey P. Ivanov, a Crimean entomologist and the scientific advisor of A. Fateryga.

Distribution. Russia (Dagestan) (Fig. 17).

Bionomics. Habitat. Imagines were observed at roadsides with richly flowering ruderal herbaceous vegetation (Fig. 18f). The road was running along a water reservoir located at the bottom of a valley. The localities 1 and 2 were situated at 575 m and 550 m a.s.l. respectively, while the mountains surrounding them were significantly higher (up to approximately 1000 m a.s.l.). The slopes of these mountains were very dry and just sparsely covered with shrubs of *Paliurus spina-christi* Mill. (Rhamnaceae). Mean annual temperature is approximately 9.1 °C, mean precipitation 592 mm (calculated for the nearby village Untsukul by https://de.climate-data.org). At both localities, the most abundant flowering plants were *Heliotropium styligerum* Trautv. (Boraginaceae), as well as *Xanthium* sp. and *X. spinosum* L. (Asteraceae). In 2019 and 2021 neither *H. styligerum* nor the wasps were found at locality 1. The third locality was situated at 1345 m a.s.l. on a slope next to a road with very sparse vegetation. The most abundant plant species was *H. styligerum* followed by *Vicia alpestris* Steven (Fabaceae).

Flower association. Adults of *Celonites ivanovi* sp. nov. visited exclusively flowers of *Heliotropium styligerum*. A total of 36 females and 1 male were recorded on flowers of this plant ("first observations"). A female visiting a flower, stood on the corolla holding on to the margins or distal parts of the petals of the same or adjacent flowers of the inflorescence with her mid- and hind-legs, while her head was situated above the corolla opening. The fore-legs were on the level surface of the corolla postero-laterally to the sides of her head. Then she rapidly protruded the proboscis thereby inserting it into the corolla tube (Fig. 18a). The proboscis was partially pro- and retracted in a high frequency, accompanied by up and down movements of the head. Immediately thereafter, pollen was transferred from the proboscis to the fore-tarsi by moving the fore-legs characteristically parallel downwards from the lower part of the head towards the corolla opening along the simultaneously retracting proboscis, while mid- and hind-legs were still used to hold on to the flower (Fig. 18b, c). Then she placed her fore-legs back on the surface of the petals, postero-laterally to the sides of her head, protruded her proboscis again into the corolla tube, and the whole sequence started anew (Fig. 18d). After a few cycles of pollen removal and transfer to the fore-tarsi, she consumed the accumulated pollen from the fore-tarsi with her mouthparts. In the process the fore-legs were alternately drawn backwards through the opened mandibles from the proximal towards the distal end of the fore-tarsi (Fig. 18e). Nectar may have been collected simultaneously with pollen, since a discrete nectar collecting behaviour was not observed. A visit to a single flower usually took just some seconds. The females walked from flower to flower of a particular inflorescence visiting several flowers one after another. Females flew between inflorescences.

Flower visits were periodically interrupted by alighting on the ground. Standing on a stone a female repeatedly regurgitated and withdrew again a mass of pollen and nectar that became visible as a droplet of liquid between her mouthparts (Fig. 18g). This behaviour may have served to thicken the pollen and nectar mass. Occasionally, females that stood on the ground were observed to brush over their heads with their fore-legs (Fig. 18h).

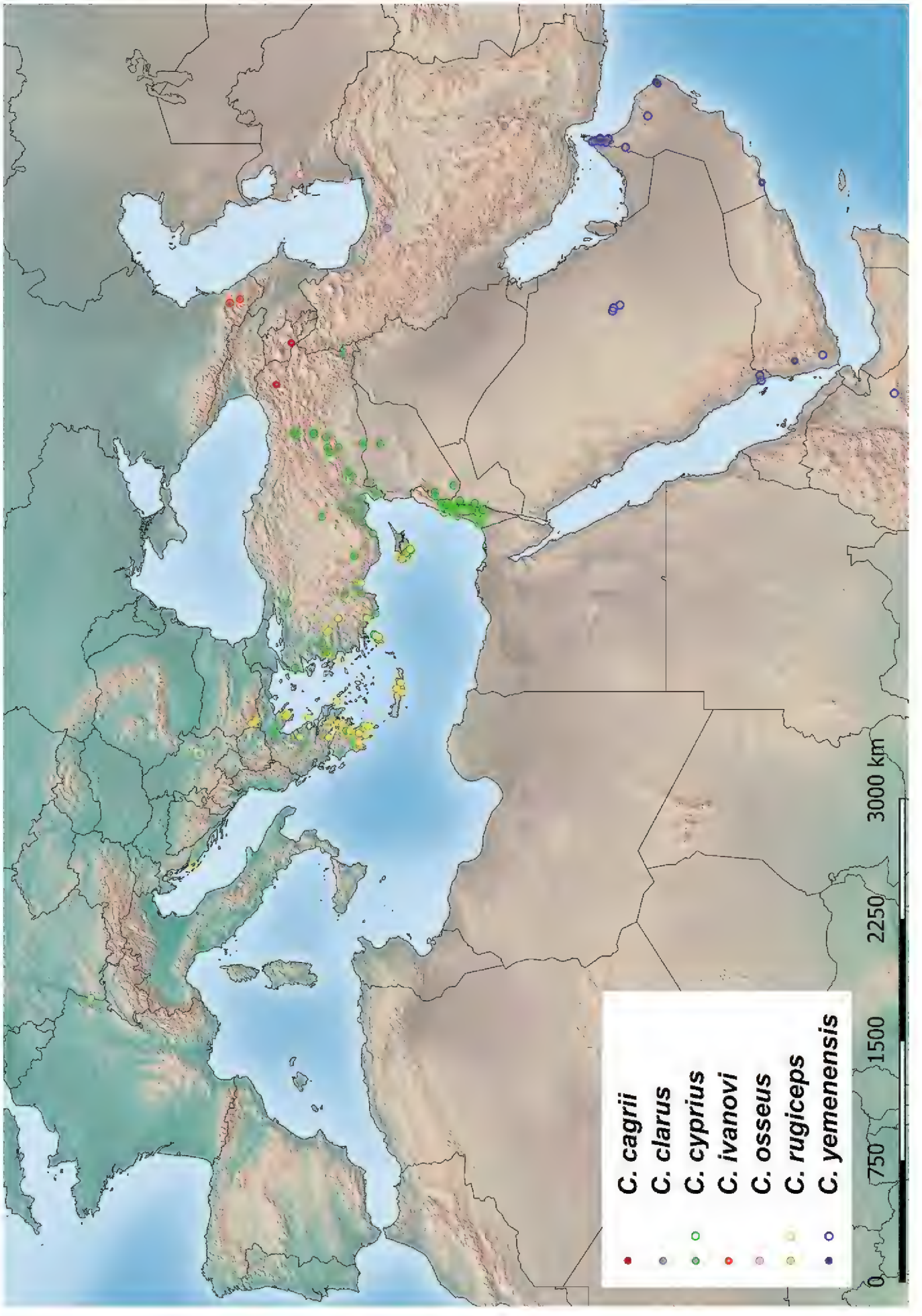

Figure 17. Geographic distribution of members of the *C. cyprius*-group (full circles specimens investigated, open circles records from literature; previously published records of *C. cyprius* from Iran and Armenia excluded; made with Natural Earth, www.naturalearthdata.com).

Figure 18. a–e, g, h Flower visiting behaviour of *Celonites ivanovi* sp. nov. females at flowers of *Heliotropium styligerum* and behaviours associated with it (details see text) **f** habitat of *C. ivanovi* sp. nov. at locality 2 in the vicinity of Maydanskoye, Dagestan **i** habitat of *C. cagrii* sp. nov. near Akşar, Turkey (aspect in autumn).

Male behaviour. Males performed patrol flights across the area covered with *H. styligerum* in a low constant flight. Patrolling was regularly interrupted by perching on the ground. Courtship and copulation were not observed.

Key to the species of the *Celonites cyprius*-group

Male of *Celonites clarus* Gusenleitner, 1973 not known.

1 Female **2**

– Male **8**

2 Larger, body length approximately 7–8 mm, more sturdily built (Fig. 1). Crenulation of terga II–IV considerably stronger (Fig. 6a). Emargination between lateral lamella and postero-lateral process of propodeum in outline comparatively small, its apical end nearly circular (Fig. 7d). Gena black. ..... ***Celonites rugiceps* Bischoff, 1928**

– Smaller, body length approximately 5–6.5 mm (Figs 1, 2). Crenulation of terga II–IV considerably weaker, sometimes almost obsolete (Fig. 6b). Emargination between lateral lamella and postero-lateral process of propodeum in outline comparatively larger, its apical end medially extended (Fig. 7a, b, e–g; except *C. cagrii* sp. nov. Fig. 7c). Gena black or with yellow marking behind compound eye **3**

3 Postero-lateral process of propodeum with blunt apical end, outline of emargination between lateral lamella and postero-lateral process narrowly elongated (Fig. 7a). Posterior margin of sternum VI nearly transverse, with sharply bended postero-lateral corners (Fig. 8a). Mesoscutum strongly reticulate with sharply raised interstices, comb-like (Fig. 6e). Head very broad, in median 1.56 times as wide as long (1.52–1.58) (Fig. 4a) ..... ***Celonites yemenensis* Giordani Soika, 1957**

– Postero-lateral process of propodeum and outline of emargination between lateral lamella and postero-lateral process different (Fig. 7b, c, e–g). Posterior margin of sternum VI more continuously curved, without distinct postero-lateral corners (Fig. 8b; less so in *C. cagrii* sp. nov. Fig. 8c). Mesoscutum reticulate, with interstices often less sharply raised and more bluntly rounded partly forming lines (Fig. 6c, d) or with dense macropunctation with smooth shiny interstices (Fig. 6f). Head in some species less broad (Fig. 4c) **4**

4 Head and especially clypeus appear less broad in frontal view, head in median 1.43 times as wide as long (1.38–1.48) (Fig. 4c). Clypeus on disk with smooth, shiny cuticula, moderately covered with fine punctures from which setae arise (Fig. 5a). Mandible on outside at base with distinct transverse depression with dull, shagreened cuticula, densely covered with pubescence of very tiny thin setae, well set off from adjacent apical smooth shiny area with few macropunctures (Fig. 5c). Fore-femur postero-ventrally only with weak carina, not produced into distinct anteriorly curved lobe in middle (Fig. 8d). Gena with extended yellow stripe behind compound eye ..... ***Celonites cyprius* Saussure, 1854**

– Head and especially clypeus appear distinctly broader in frontal view, head at least 1.45 times as wide as long (Fig. 4b, d–f). Clypeus on disk with some coarser depressions i.e. dorso-laterally, where punctures are in rows and

interstices are slightly raised forming wrinkled lines; setae arise from larger punctures (Fig. 5b). Mandible on outside at base without distinct transverse depression, basal area with shagreened cuticula extending further apically, dorsal to condylar ridge becoming distinctly longitudinally striated, basally moderately covered with pubescence of tiny thin setae (longer than in *C. cyprius*); this area contrasts to smooth shiny cuticula on condylar ridge and ventro-apical outside (Fig. 5d). Fore-femur postero-ventrally produced in middle into distinct anteriorly curved lobe that distally changes into tapering carina along ventral margin of femur (Fig. 8e, f). Gena black or with yellow marking behind compound eye..... **5**

5 Mesoscutum with dense macropunctation with smooth shiny interstices (Fig. 6f). A3 shorter, in median 2.1 times as long as wide (Fig. 15a). Postero-lateral process of propodeum with blunter apical end, outline of emargination between lateral lamella and postero-lateral process with narrow elongated neck (Fig. 7b). Crenulation along posterior margin of metasomal terga weak and blunt, not exceeding the lower hyaline rim of the tergum (Fig. 2). Gena with yellow marking in middle behind outside bend of compound eye and sometimes additional yellow spot close to mandible. Head very broad, in median 1.56 times as wide as long (1.55–1.56) (Fig. 4b)..... ..... ***Celonites clarus* Gusenleitner, 1973**

– Mesoscutum reticulate, with distinctly raised narrow interstices partly forming lines (Fig. 6c, d). A3 longer, in median 2.5 times as long as wide (Fig. 15b). Postero-lateral process of propodeum with converging end (Fig. 7e–g). Gena black or with yellow marking..... **6**

6 Outline of emargination between lateral lamella and postero-lateral process of propodeum with narrow short neck, its apical end small oval-shaped (Fig. 7c). Anterior pronotal carina short, forming anterior sharp edge along ventral half of crenate groove. Crenate groove straight, trough-like, its nearly vertical posterior wall separated from posterior margin of pronotum by a stripe of cuticula similarly covered with micropunctures and at same level as surface of surrounding antero-ventral area of pronotum. Bulged shiny rim of sternum VI postero-laterally strongly curved in medial direction, running obtuse to nearly transverse at posterior end resulting in blunter appearance of posterior end of sternum VI (Fig. 8c). Posterior section of bulged rim of sternum VI partly interrupted by large depressions of macropunctures (Fig. 8c). Dorso-posterior margin of sternum VI with distinct irregularly serrated crystalline horizontal lamella situated immediately above posteriorly directed stiff setae, dorso-medially fused with median spine and somewhat more protruded at postero-lateral edges (Fig. 8h, i). Light markings light yellowish-white. Head broad, in median 1.50 as wide as long (1.45–1.54) (Fig. 4f)..... ..... ***Celonites cagrii* Mauss & Yildirim, sp. nov.**

– Outline of emargination between lateral lamella and postero-lateral process of propodeum with broad short neck, its apical end medially enlarged (Fig. 7f, g).

Anterior pronotal carina starts close to posterior margin of pronotum and runs in short parabolic curve antero-laterally and then parallel to posterior margin of pronotum forming anterior margin of crenate groove. Anterior pronotal carina fairly projecting in posterior direction over anterior border of groove, especially along its ventral parabolic curve. Crenate groove posteriorly open, posteriorly adjacent cuticula gradually rising to posterior margin of pronotum. Cuticula in this lowered area differs from surrounding surface of antero-ventral area of pronotum being obliquely striated with some folds that are ±continuing into bottom ribs of crenate groove. Bulged shiny rim of sternum VI forms regular curve postero-laterally resulting in more pointed appearance of posterior end of sternum VI (Fig. 8b). Posterior section of bulged rim of sternum VI not or barely interrupted by large depressions of macropunctures (Fig. 8b). Dorso-posterior margin of sternum VI at most with simple weak translucent cuticula crest (Fig. 8g). Light markings yellowish-white or yellow..... **7**

7 Head in frontal view more triangular, outline of compound eye less strongly curved (Fig. 4e), in median 1.48 as wide as long (1.45–1.53). Light colouration yellowish-white, less extended, normally mesoscutum black (Fig. 6c) and outside of mid- and hind-tibia with dark ring-like markings. Dark colour of head and mesosoma deep black (Fig. 2)..... ***Celonites ivanovi*** **Mauss & Fateryga, sp. nov.**

– Head in frontal view more elliptic, outline of compound eye nearly semi-circular (Fig. 4d), in median 1.57 as wide as long (1.50–1.62). Light colouration more yellowish to yellow, more extended, with yellow spot on mesoscutum (Fig. 6d) and outside of mid- and hind-tibia completely yellow. Dark colour of head and mesosoma black, partly with more or less brownish to reddish shade (Fig. 2) ..... ***Celonites osseus*** **Morawitz, 1888**

8 Larger, body length approximately 7–8 mm, more sturdily built (Fig. 1). Sternum VIII semicircularly produced, not emarginated (Fig. 14a). Male genital as in Figs 10a, 11a. Harpide ventrally at base with unique ventro-medially extending sclerite (Figs 12a, 13a) ..... ***Celonites rugiceps*** **Bischoff, 1928**

– Smaller, body length approximately 5–6.5 mm (Figs 1, 2). Sternum VIII acutely produced, running into two tapering lobes at posterior end with deep median incision between them (Fig. 14b–f). Male genital different (Figs 10b–f, 11b–f). Harpide ventrally at base without ventro-medially extending sclerite (Figs 12b–f, 13b–f)..... **9**

9 Posterior lobes of sternum VIII of medium length, wedge-shaped with acute-angled end (Fig. 14b). Male genital along posterior end of ventral plate of stipes with dense band of conspicuously long strong setae projecting well above volsella (Figs 12b, 13b). Ventral side of harpide densely covered with long setae (Figs 12b, 13b) ..... ***Celonites cyprius*** **Saussure, 1854**

– Posterior lobes of sternum VIII different (Figs 14c–f). Male genital on ventral plate of stipes at most with a sparse row of short setae (Figs 12c–f, 13c–f). Ventral side of harpide less densely covered with shorter setae (Figs 12c–f, 13c–f)..... **10**

10 Posterior lobes of sternum VIII short with blunt ending (Fig. 14c). Male genital as in Figs 10c, 11c, 12c, 13c. Lateral margin of harpide strongly and continuously concave along most of its length ..... ***Celonites yemenensis* Giordani Soika, 1957**

– Posterior lobes of sternum VIII long, lanceolate with pointed tip (Fig. 14d–f). Male genital as in Figs 10d–f, 11d–f, 12d–f, 13d–f. Lateral margin of harpide with concavity at most along posterior half of its length..... **11**

11 Male genital broader at base (Figs 10d, 11d), cupula wider, less curved (in ventral view; Figs 12d, 13d). Lateral margin of harpide without concavity near apical end, due to broad lamella along postero-lateral margin of harpide (Figs 12d, 13d). Median lobe of tergum VII broader at base between postero-lateral angles (Fig. 9c) ..... ***Celonites osseus* Morawitz, 1888**

– Male genital narrower at base (Figs 10e, f, 11e, f), cupula narrower, more strongly curved (in ventral view; Figs 12e, f, 13e, f). Lateral margin of harpide with shallow concavity near apical end. Median lobe of tergum VII narrower at base between postero-lateral angles (Fig.10 d, e)..... **12**

12 Head in frontal view more triangular (Fig. 9a). Antennal club (A8–12) in dorsal view about 1.8–1.9 times as long as broad, asymmetrical, with evenly rounded anterior margin and weakly concave distal margin that is running obliquely upwards. At postero-distal edge distal margin curved into posterior margin forming a blunt angle (Fig. 9f); posterior margin weakly convex. Median lobe of tergum VII markedly produced, its posterior margin and adjacent posterior translucent lamella entirely convex (Fig. 9d). Sternum VIII with longitudinal depression in centre largely oval, lancet-like tips and postero-median incision between them broader (Fig. 14e). Aedoeagus with narrowly rounded distal end, its lateral sides noticeably converging. Uncus thyrsos sharp (Fig. 12e). Apodema thyrsos robust, anteriorly curved laterad (Figs 10e, 11e). Outline of emargination between lateral lamella and postero-lateral process of propodeum with broad short neck, its apical end medially enlarged (Fig. 7g). Yellowish-white stripe antero-medial on antenna restricted to A3–A7, at most with light brownish shade on adjacent proximal margin of A8..... ***Celonites ivanovi* Mauss & Fateryga, sp. nov.**

– Head in frontal view strongly oval (Fig. 9b). Antennal club (A8–12) in dorsal view about 1.68 times as long as broad, asymmetrical, with evenly rounded anterior margin and straight distal margin, that is running transverse. At postero-distal edge distal margin bent into posterior margin at nearly right angle (Fig. 9g); posterior margin nearly straight. Median lobe of tergum VII moderately produced, its posterior margin weakly concave in middle, with adjacent posterior translucent lamella fairly emarginated (Fig.10e). Sternum VIII with longitudinal depression in centre more elongated, lancet-like tips and postero-median incision between them narrower (Fig. 14f). Aedoeagus with broadly rounded distal end, its lateral sides only weakly converging. Uncus thyrsos comparatively broad and blunt (Fig. 12f). Apodema thyrsos delicate,

anteriorly nearly straight (Figs 10f, 11f). Outline of emargination between lateral lamella and postero-lateral process of propodeum with narrow neck, its apical end small oval-shaped (Fig. 7c). Yellowish-white stripe antero-medial on antenna continues on proximal part of A8 ..... ***Celonites cagrii*** **Mauss & Yildirim, sp. nov.**

Geographic distribution

The distribution of the members of the *C. cyprius*-group is shown in Fig. 17. All of the 20 studied specimens from collection sites in Iran and Armenia that previously had been determined as *C. cyprius smyrnensis* Richards, 1962 by J. Gusenleitner turned out to belong to *C. osseus* (dbM 4617, 5675–5679, 5778–5788) and *C. cagrii* sp. nov. (dbM 5789, 5790) respectively or even to *C. clarus* (dbM 4616). For that reason, the occurrence of *C. cyprius* is considered as doubtful in Iran and Armenia and all of the nine published records of *C. cyprius* from both countries by Gusenleitner (1973, 1997) and Ebrahimi and Carpenter (2008) were excluded from the data set. *Celonites rugiceps* seems to be absent from the whole Levant region (Fig. 17). Reinvestigation of a single specimen from Jordan (dbM 2523) previously reported by Mauss and Prosi (2013) to represent *C. rugiceps* revealed that it was misidentified and belongs to *C. cyprius* instead.

Discussion

Celonites cagrii sp. nov., *C. ivanovi* sp. nov. and *C. osseus* can be assigned to *Eucelonites* and to the *Celonites cyprius*-group without contradictions since the imagines share the potential apomorphic characters of these taxa, that is the axilla is produced into a curved tapering projection which fits into a slight emargination of the tegula (Richards 1962) and the harpide has a tapering spatula-like distal end with a vertical duplication ventrally along the medial margin. Within the *Celonites cyprius*-group *C. cagrii* sp. nov., *C. ivanovi* sp. nov. and *C. osseus* are especially similar in most morphological characters. Therefore they are probably closely related and we suggest naming this group the *C. osseus*-complex. The close relationship of the members of the *C. osseus*-complex is supported by the COI-5P sequence analyses that revealed that within the *C. cyprius*-group the lowest interspecific genetic distances exist between *C. ivanovi* sp. nov. and *C. cagrii* sp. nov., while they differ from the available sequences of the other species by at least 11% (Fig. 16). However, the COI-5P gene sequence of *C. osseus* is still unknown, so that the close relationship of *C. osseus* to *C. cagrii* sp. nov. and *C. ivanovi* sp. nov. deduced from morphological data cannot be proved genetically at the moment.

Celonites osseus differs from *C. cagrii* sp. nov. and *C. ivanovi* sp. nov. in the shape of the harpides and the base of the male genital which is associated with different proportions of tergum VII and sterna VII+VIII of the males. Differences between *C. cagrii* sp. nov. and *C. ivanovi* sp. nov. exist in the form of the male antennal club, the proportions

of tergum VII and sternum VIII, as well as some structures of the aedoeagus. All of these characteristics can be assumed to be associated with mating behaviour in *Celonites* (cf. Mauss 2006; Mauss and Müller 2014). Thus it can be hypothesized that the dissimilarity between these traits functions as a reproductive isolation mechanism between the taxa so that they probably constitute different biospecies *sensu* Mayr (1967). This hypothesis is corroborated by the measured mean interspecific genetic distance between *C. cagrii* sp. nov. and *C. ivanovi* sp. nov. of more than 7%. In Central European Apoidea and Vespoidea a level of COI sequence divergence exceeding 2% commonly signals different species, although there are a few exceptions in which maximum intraspecific genetic distances of up to 13.1% are not correlated with equally pronounced morphological characters (Schmidt et al. 2015; Schmid-Egger and Schmidt 2021).

Besides other morphological characteristics many species of the *C. cyprius*-group vary in the shape of the postero-lateral process and the lateral lamella of the propodeum resulting in different outlines of the emargination between them. Species specific differences in the shape of the postero-lateral part of the propodeum were already observed between *C. cyprius*, *C. rugiceps* and *C. clarus* (Richards 1962; Gusenleitner 1973), and also exist among another four Palaearctic (Gusenleitner 1973) and four Afrotropical species of *Celonites* (Gess 2007). The function of this structure is unknown and therefore its contribution to reproductive isolation is unclear. Nevertheless, the repeated observation of species-specific differences in the postero-lateral part of the propodeum within *Celonites* suggests that the distinct structures are associated with an unknown mechanism of reproductive isolation or niche segregation. Hence, it is of note that *C. cagrii* sp. nov. differs distinctly in this character from *C. ivanovi* sp. nov. and *C. osseus* that, for their part, resemble *C. cyprius*.

The relation of *Celonites clarus* to the *C. cyprius*-group is still unresolved. It is only known from the type series collected near Teheran (Gusenleitner 1973; Rahmani et al. 2020) and the single female from Kerman province in south-east Iran assigned to this species in this study. In accordance with the description by Gusenleitner (1973) this female and two investigated paratype specimens differ distinctly from all other members of the *C. cyprius*-group in the structure of the cuticula on frons and mesoscutum and the unique postero-lateral part of the propodeum. On the other hand, *C. clarus* is otherwise quite similar to the members of the *C. osseus*-complex apart from having comparatively shorter antennae and a weaker or even absent crenulation along the posterior margins of the metasomal terga. Since the male of *C. clarus* is still unknown and genetic data are unavailable, the position of the taxon within *Eucelonites* remains uncertain and should be reinvestigated with care, when more material becomes available.

Celonites ivanovi sp. nov. and *C. cagrii* sp. nov. were exclusively recorded from flowers of different *Heliotropium* species. This corresponds to other members of the *C. cyprius*-group for which flower visiting records are available, that is *C. cyprius* and *C. rugiceps*, that were also found at flowers of various *Heliotropium* plants (Richards 1962; Mauss pers. obs.). The behaviour of *C. ivanovi* sp. nov. during pollen uptake from *H. styligerum* flowers is very similar to the behaviour of *C. cyprius* and *C. rugiceps* at flowers of other *Heliotropium* species (Mauss pers. obs.). Therefore, it is probably homologous.

The geographic range of *Celonites osseus* is similar to Iranian faunal elements *sensu* Lattin (1967). The adjacent small and probably endemic distribution areas of the closely related *C. ivanovi* sp. nov. and *C. cagrii* sp. nov. on the northern side of the Greater Caucasus and in East-Anatolia and Armenia respectively can be hypothesized to be relicts of a previous interglacial range expansion of their last common ancestor shared with *C. osseus*. In the following glacial epoch, range regression probably resulted in geographic isolation of small relict populations that evolved into separate biospecies. Postglacially *C. ivanovi* sp. nov. and *C. cagrii* sp. nov. remained in their glacial refuges, while *C. osseus* expanded its range again. The other species of the *C. cyprius*-group can also be assigned to different glacial refuges *sensu* de Lattin (1967) with *C. rugiceps* and *C. cyprius* being of Ponto-Mediterranean origin, while *C. yemenensis* has a distinct Syroeremial distribution and *C. clarus* seems to represent the Iranoeremial type. This distribution pattern indicates that speciation within the *C. cyprius*-group was most likely influenced by geographic isolation during glacial periods. The sympatric occurrence of *C. cyprius* with *C. rugiceps* in the west and of *C. osseus* with *C. clarus* in the east implies that some kind of niche segregation evolved between these taxa.

Just three species of pollen wasps (all in the genus *Celonites*) were previously known from Russia (Antropov and Fateryga 2017; Fateryga 2020). The present contribution increases this number to four. Since the known distribution ranges of *C. ivanovi* sp. nov. and *C. cagrii* sp. nov. are very restricted, both species may be endangered. Therefore, a systematic search for further localities of *C. ivanovi* sp. nov. in the Caucasus or *C. cagrii* sp. nov. in East Anatolia and Armenia should be carried out in suitable habitats with occurrence of *Heliotropium* plants.

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Supplementary material 1

Supplementary material

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Data type: investigated specimens, published records, localities

Explanation note: List of all specimens, published records and localities included in the study.

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